

A new Cambrian (Jiangshanian, Sunwaptan) trilobite fauna from Oklahoma and its biostratigraphic significance.

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Non-technical summary.—A newly discovered trilobite fauna from the Cambrian Honey Creek Formation marks a distinct interval that follows an extinction event. Dominated by the genus *Monocheilus* in association with *Ptychaspis*, it resembles faunas from Alberta, Canada, and the Upper Mississippi Valley region of the United States. *Ptychaspis bullasa* Lochman and Hu, 1959 is a species that has been reported widely in North America. However, restudy of various museum collections shows that the various occurrences record a set of more narrowly distributed species. The pattern of distribution is similar to groups of modern “pseudocryptic species” identified by a combination of genetic and anatomical data.

Abstract.—The Cambrian (Jiangshanian, Sunwaptan) Honey Creek Formation in the Wichita Mountains region of Oklahoma yielded a new fauna dominated by *Monocheilus* Resser, 1937 (senior synonym of *Stigmacephalus* Resser, 1937) in association with *Ptychaspis* Hall, 1863. It occupies the same stratigraphic position as similar faunas in the Upper Mississippi Valley and Alberta, lying a little above an interval characterized by species of *Taenicephalus* Ulrich and Resser in Walcott, 1924 and *Orygmaspis* Resser, 1937. Revision of *Ptychaspis bullasa* Lochman and Hu, 1959 from type material from Idaho and sclerites attributed to the species from Texas reveals a plexus of pseudocryptic species that share tuberculate sculpture on the cranium. New species are *Monocheilus reginae*, *Monocheilus richardi*, *Ptychaspis occulta*, and *Ptychaspis matuszaki*.

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Introduction

Cambrian trilobites of Oklahoma have been studied intensively for 70 years (e.g., Frederickson 1948, 1949; Stitt, 1971, 1977; Westrop et al., 2010), so it is surprising to discover an entirely new fauna in the succession. This fauna is of interest because it includes early representatives of two major clades (Ptychaspidae Raymond, 1924 and Eurekaidae Hupé, 1953) that radiated in Laurentia during the Sunwaptan Stage. The composition of the fauna, which is dominated by *Monocheilus* Resser, 1937 and also contains *Ptychaspis* Hall, 1863, resembles assemblages that occur in the same homotaxial position in Minnesota and Wisconsin (e.g., Nelson, 1951) and in the southern Canadian Rocky Mountains (Westrop, 1986). As such, these assemblages may mark a distinct biostratigraphic interval in a transition from low-diversity faunas in the aftermath of the end-Steptoean extinction to more-diverse Sunwaptan faunas (e.g., Westrop and Cuggy, 1999).

Monocheilus (considered here to be a senior synonym of *Stigmacephalus* Resser, 1937; see Systematic paleontology, which follows) is the earliest representative of the family Eurekaidae, and the occurrence of *Ptychaspis* is likely the oldest record of the family Ptychaspidae. Early representatives of

Ptychaspis have often been assigned to a single species, *P. bullasa* Lochman and Hu, 1959 (e.g., Bell and Ellinwood, 1962; Stitt, 1971, 1977). Restudy of type material shows that there is in fact a plexus of pseudocryptic species (e.g., Westrop and Adrain, 2007; Westrop et al., 2018) that are differentiated readily by cranial and pygidial anatomy (see Systematic paleontology).

Stratigraphy and study area

The study area lies in the Slick Hills, immediately north of the Wichita Mountains. The Honey Creek Formation and the underlying Reagan Sandstone compose the Timbered Hills Group (Stitt, 1971). The Timbered Hills overlaps the Carlton Rhyolite, which was exposed in late Cambrian Oklahoma as a volcanic archipelago with at least 300 m of relief (Donovan, 1986; Donovan and Bucheit, 2000; Donovan et al., 2000). The boundary between the Reagan and the Honey Creek is gradational through an interval of sandstone with bioclastic carbonate interbeds and lenses. Following Donovan and Ragland (1986), we place the base of the Honey Creek at the lowest occurrence of bioclastic carbonate, and this definition differs from the one offered by Stitt (1977, p. 5), who placed the boundary above the highest sandstone interbed. Lithologically, the formation is a pelmatozoan-rich, glauconitic, bioclastic grainstone and rudstone with thin siliciclastic drapes. Cross-bedding and ripple

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marks are common, as are sandstone interbeds. Heterolithic intervals are composed of fine- to medium-grained sandstone with recessively weathering bioclastic carbonate lenses (Westrop et al., 2010, fig. 1). Bucheit and Donovan (2000, fig. 16) interpreted the Honey Creek as a tidally influenced deposit that formed between rhyolite islands.

The Fort Sill Formation (lowest unit of the Arbuckle Group) succeeds the Honey Creek Formation and is composed of lime mudstone–wackestone (Stitt, 1971; Donovan and Ragland, 1986). Intraclastic rudstone is also present, and microbial buildups occur in the upper part of the formation (Stitt, 1971). Quartz sand and glauconite are minor components, suggesting that the archipelago was largely flooded during deposition of the Fort Sill.

The trilobites were collected from the succession in the Bally Mountain region (section BM) of Kiowa County, which was deposited near a rhyolite island (Donovan and Bucheit, 2000). The section (Fig. 1.1) was measured and logged on the west-facing slope of an unnamed ridge about one kilometer to the east of Bally Mountain (Fig. 1.2, 1.3; 34°57'39"N, 98°39'03"W). *Elvinia* Zone faunas are well represented in a carbonate unit about 52.5 m above the base of the section. An overlying 12 m sandstone unit did not yield trilobites, but *Taenicephalus wichitaensis* Resser, 1942 and *Conaspis testudinata* Ellinwood in Bell and Ellinwood, 1962 are present in the succeeding carbonate unit, between 70.5 m and 72 m above the base of the section (Fig. 1.1); the systematics of these species will be treated elsewhere. The newly discovered, low-diversity fauna dominated by new two species of *Monocheilus*, *M. reginae* and *M. richardi* (Figs. 2–6), occurs about 8 m higher in the section, in the Honey Creek–Fort Sill boundary interval (Fig. 1.1). It is referred to here as the *Monocheilus reginae* fauna.

Ptychaspis is rare at the Bally Mountain section, and our study includes archival material from elsewhere in Oklahoma as well as Texas and Idaho. The type material of *P. matuszaki* n. sp. was collected from exposures of the Fort Sill Formation, along a section-line road 4.4 km southeast of Hennepin (SE Sec. 4, T1S, R1W; 34°29'46"N, 97°18.0'4"W) separating sections 3 and 4, Murray County, Oklahoma (Matuszak, 1957). This site is 450 m northeast of section DR of Westrop and Adrain (2007, p. 989, fig. 1c). Sclerites assigned to *P. occulta* n. sp. and *Ptychaspis* spp. are from the Morgan Creek Member, Wilberns Formation, central Texas, and were illustrated previously by Bell and Ellinwood (1962) and Longacre (1970) under the name *Ptychaspis bullasa* Lochman and Hu, 1959. Revision of *P. bullasa* is based on restudy of the type material from the Mink Creek region, near Preston, southern Idaho (Lochman and Hu, 1959).

Age and correlation of the *Monocheilus reginae* fauna

The *Monocheilus reginae* fauna occurs in two collections (Fig. 1.1). The lower of these (BM 79.4T) is a float sample of trilobite grain- to rudstone from a covered interval 1.6 m below the base of the Fort Sill Formation. It includes abundant sclerites of *Monocheilus* and rare specimens of *Ptychaspis* and *Wilbernia* Walcott, 1924. Collection BM 80.7 is lithologically similar to BM 79.4T but was recovered in place 1.3 m higher in the section and 30 cm below the base of the Fort Sill.

Monocheilus and *Ptychaspis* are both minor components of this collection, with *Minkella* Lochman and Hu, 1959 dominating. The latter genus is under study by S.R.W. and will not be treated in this paper.

Both species of *Monocheilus* described in this paper are related to *M. oweni* (Hall, 1863). However, that species is based on sandstone internal molds that provide no information on such features as sculpture of the exoskeleton and, as a result, is difficult to evaluate. It is best restricted to the types (see discussion of *M. richardi* that follows), and we use the shutter-mark convention (Wiley, 1979) in the following discussion to underscore uncertainty about reports of the species in various regions. *Monocheilus* “*oweni*” (under the name *Stigmacephalus*) has been reported from a collection (B57) from the Bison Creek Formation of Alberta (Westrop, 1986), which, as in Oklahoma, also includes *Ptychaspis* and a species of *Wilbernia*. Westrop (1986, p. 17) placed this collection in his *Stigmacephalus oweni* fauna, which encompassed a poorly fossiliferous interval whose base was defined broadly by the first occurrences of either the name-bearing species, *Idahoia* cf. *I. lirae* (Frederickson, 1949) or *Taenicephalina* sp. 1. *Idahoia* cf. *I. lirae* is distinct from Frederickson’s types of *I. lirae* from Oklahoma (Westrop, 1986, pl. 16, figs. 5–7) by virtue of, among other characters, a long occipital spine (Westrop, 1986, p. 42). This species does not co-occur with *M. “oweni”* in any of Westrop’s (1986) sections: *Idahoia* cf. *I. lirae* occurs in his section D, whereas *M. “oweni”* is from his sections B and S. As a result, there is some uncertainty about the relative ranges of these two species, although *M. “oweni”* seems to extend into younger strata (see Westrop, 1986, p. 18 for discussion). In Oklahoma, the *M. reginae* fauna lies above the *I. lirae* Zone, which is present in the Honey Creek Formation about 16 km to the southeast at section KR1 (see Westrop et al., 2010 for locality information), 3.1 m above the highest occurrence of *Taenicephalus wichitaensis* Resser, 1942 (unpublished data, Blackwell and Westrop, 2023). The evidence suggests that the ranges of *M. reginae*, *M. richardi*, and *M. oweni* likely overlap, and the *M. oweni* fauna and the *M. reginae* fauna may be broadly correlative.

In the Minnesota–Wisconsin border region of the St. Croix Valley (Nelson, 1951), *M. “oweni”* occurs above the *Conaspis* Zone (= *Taenicephalus* Zone; Grant, 1965), confirming that this species is among the older representatives of the genus. Sections farther to the south, along the bluffs of the Mississippi (Grant, 1962), apparently lie above the local range of *M. “oweni”* and instead contain *M. anatinus* (Hall, 1863) in association with *Ellipsocephaloides curtus* (Whitfield, 1878) and *Idahoia wisconsinensis* (Owen, 1852) (e.g., Grant, 1962, text-figs. 3, 6), among others. Both of the latter two species enter the succession in Alberta above the *M. oweni* fauna (Westrop, 1986).

Materials and methods

Unless indicated otherwise, treatment of each species is based on the figured specimens. Specimens were coated with a sublimate of ammonium chloride before photography. Depth of field was maximized by rendering digital images from stacks of images focused at 100 μm intervals using Helicon Focus 4.0 for the Macintosh <<http://www.heliconsoft.com>>. Proportions

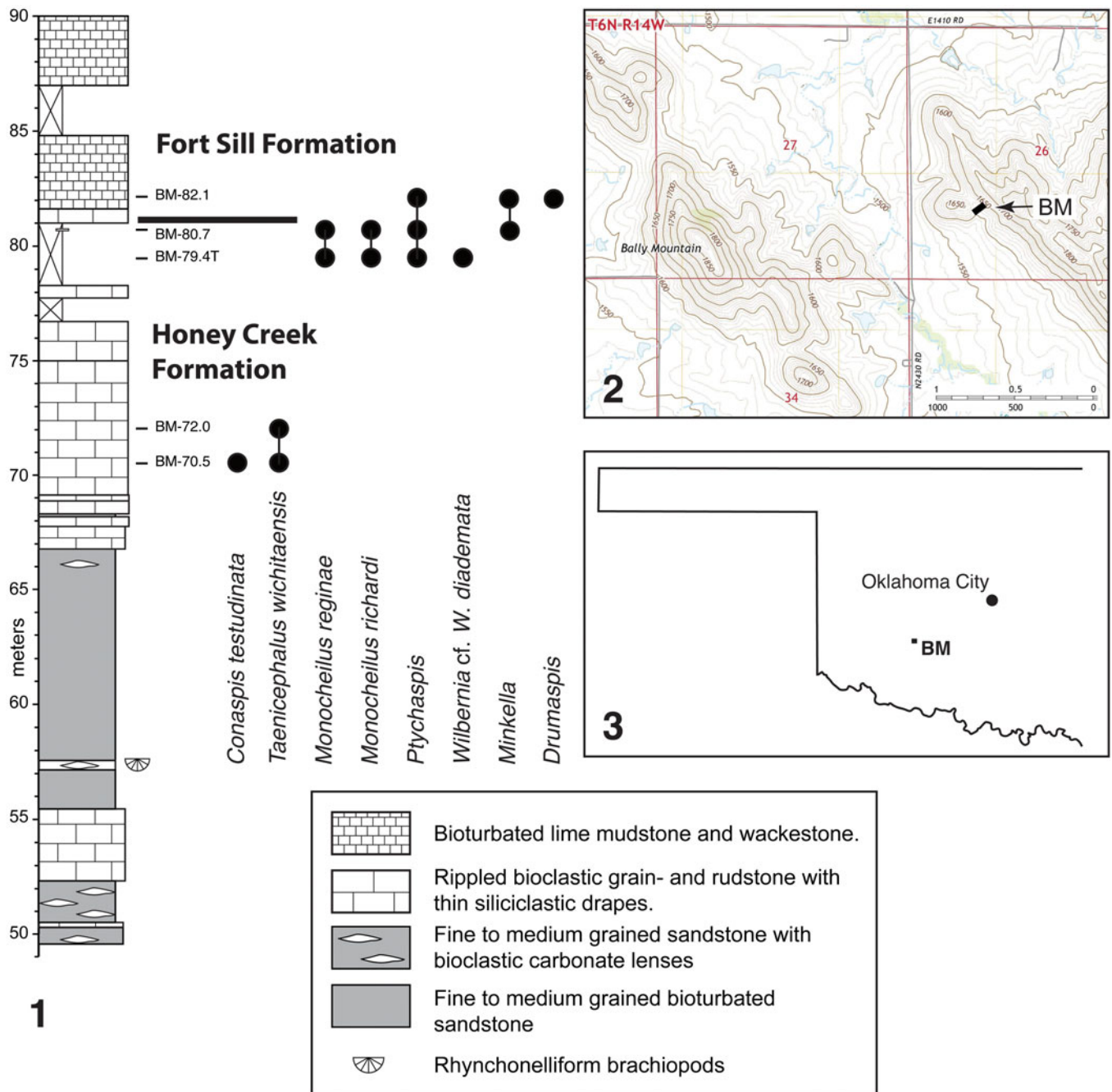


Figure 1. (1) Stratigraphic column and species range chart for the Honey Creek–Fort Sill boundary interval, Bally Mountain section (BM), Kiowa County, Oklahoma. (2) Map showing the location of the section. (3) Map showing location of the study area in Oklahoma.

expressed in percentages in descriptions and diagnoses are means, with the following pair of numbers indicating the range of values. All measurements were made on digital images to the nearest tenth of a millimeter using the Measure Tool of Adobe Photoshop.

Repositories and institutional abbreviations.—Illustrated specimens are housed at the Oklahoma Museum of Natural History, University of Oklahoma, Norman (OU), and at the National Museum of Natural History, Washington D.C. (USNM).

Systematic paleontology

Family Eurekaidae Hupé, 1953

Remarks.—Adrain and Westrop (2004, p. 19) raised the possibility that *Monocheilus* Resser, 1937 and *Stigmacephalus* Resser, 1937 were related to younger Sunwaptan genera assigned to the family Eurekaidae. As discussed in the following, these genera are considered to be synonyms, and Resser (1937) published both names in the same publication. As first revisers, we choose *Monocheilus* as the senior

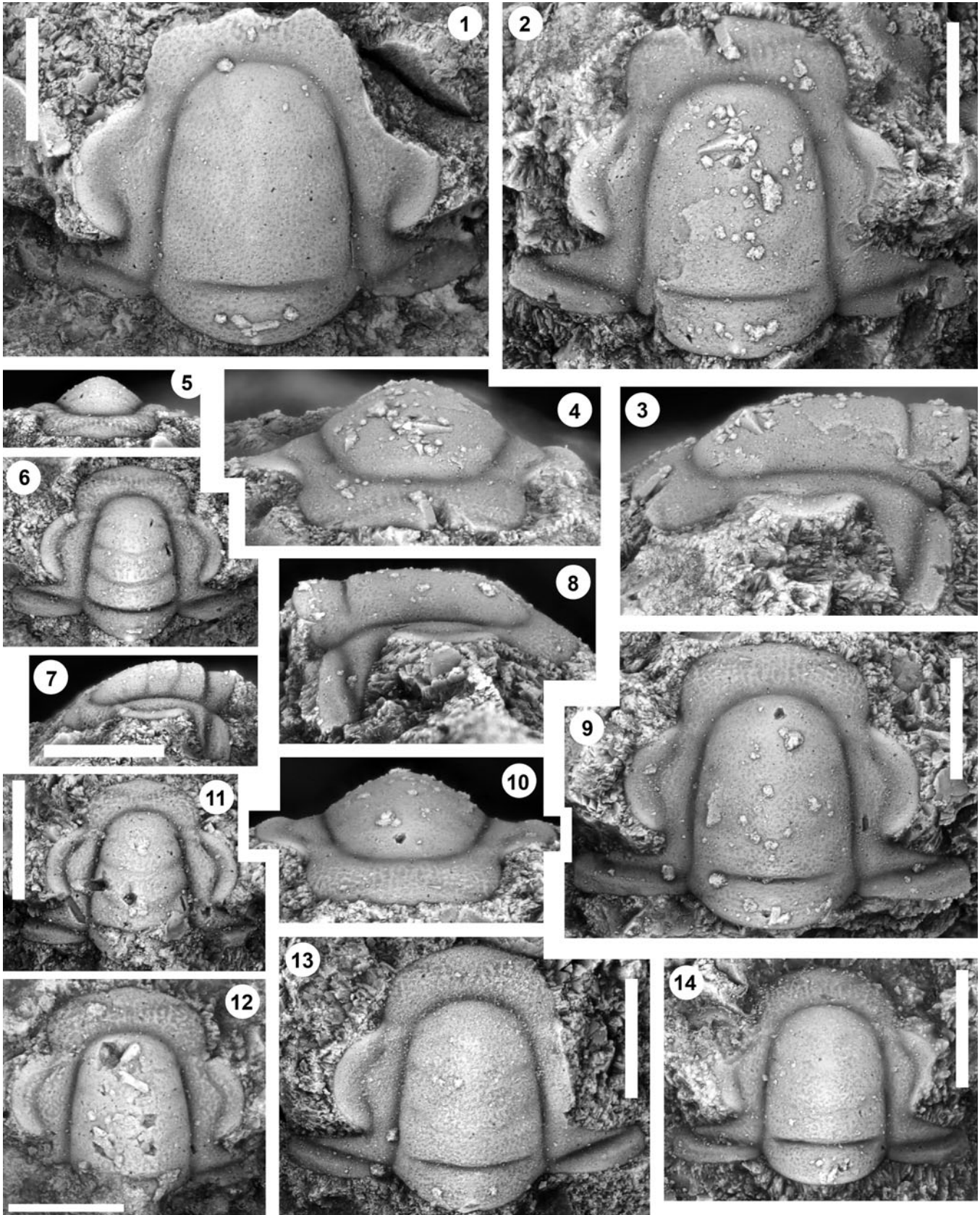


Figure 2. *Monocheilus reginae* n. sp. from the uppermost Honey Creek Formation, Bally Mountain section, Kiowa County, Oklahoma. All are cranidia from collection BM 79.4T. All are paratypes. (1) OU 238356, dorsal view. (2–4) OU 238357: (2) dorsal view; (3) lateral view; (4) anterior view. (5–7) OU 238358: (5) anterior view; (6) dorsal view; (7) lateral view. (8–10) OU 238359: (8) lateral view; (9) dorsal view; (10) anterior view. (11) OU 238360, dorsal view. (12) OU 238361, dorsal view. (13) OU 238362, dorsal view. (14) OU 238363, dorsal view. Scale bars = 1 mm.

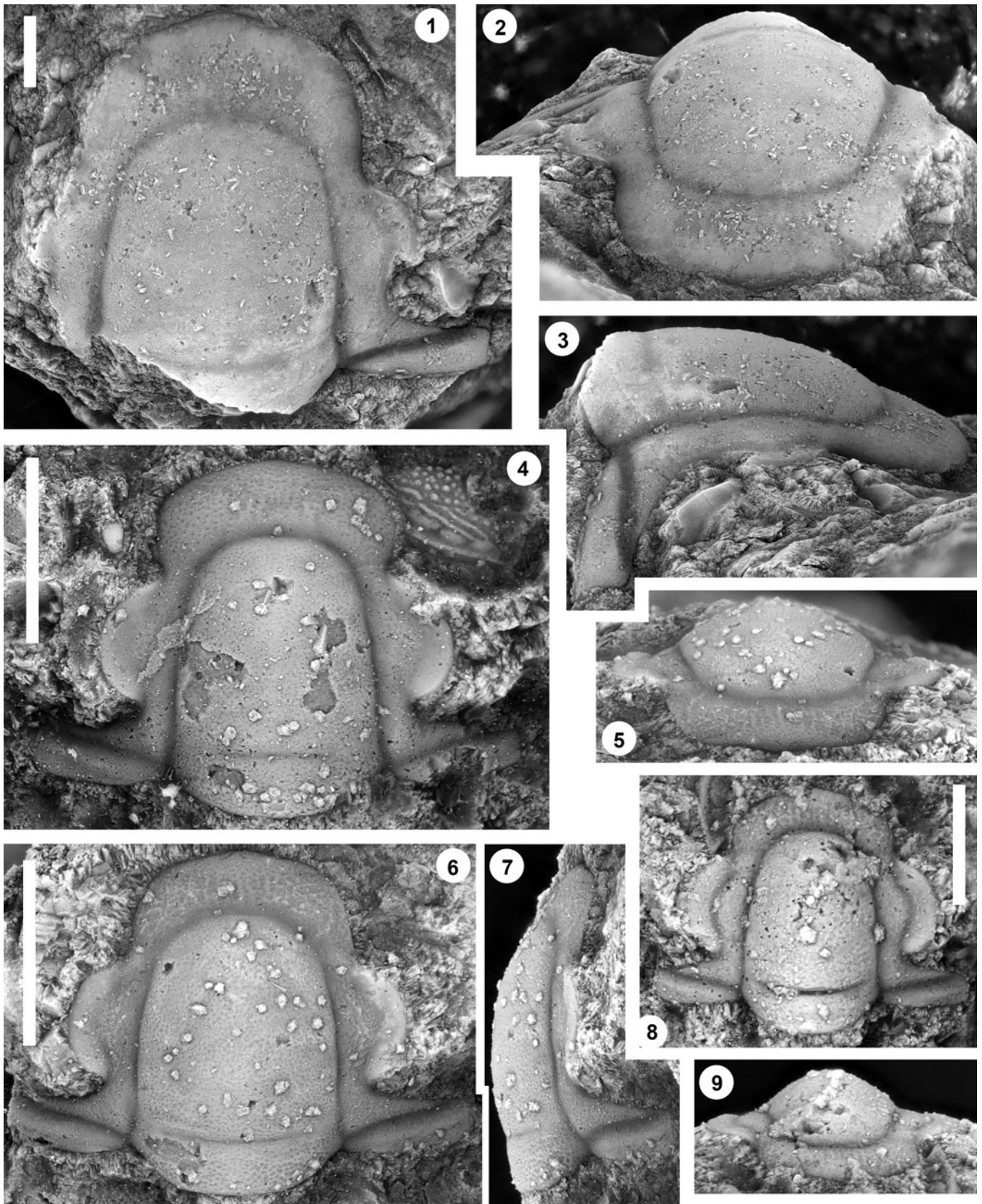


Figure 3. *Monocheilus reginae* n. sp. from the uppermost Honey Creek Formation, Bally Mountain section, Kiowa County, Oklahoma. All are crania from collection BM 79.4T. (1–3) Paratype OU 238364: (1) dorsal view; (2) anterior view; (3) lateral view. (4) Paratype OU 238164, dorsal view. (5–7) Holotype OU 238158: (5) anterior view; (6) dorsal view; (7) lateral view. (8, 9) paratype OU 238365: (8) dorsal view; (9) anterior view. (1–7) Scale bars = 2 mm; (8, 9) scale bar = 1 mm.

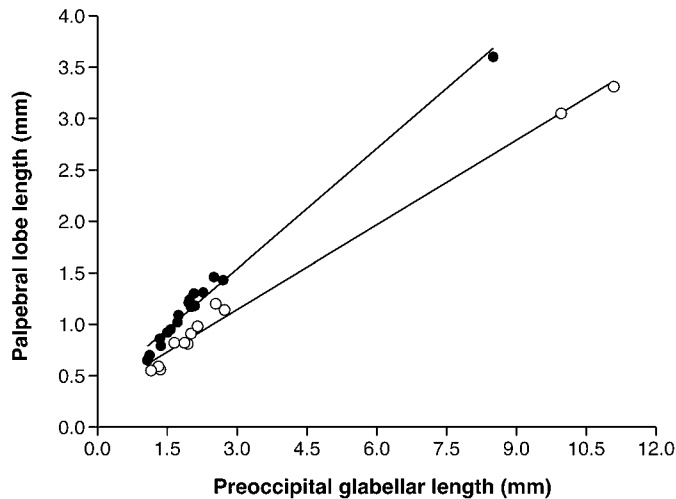


Figure 4. Plot of palpebral lobe length against preoccipital glabellar length for *Monocheilus reginae* (black fill) and *M. richardi* (white fill). Reduced major axis regression lines were fitted in PAST v.4.09 (Hammer et al., 2001). For *M. reginae*, $y = 0.39x + 0.37$; for *M. richardi*, $y = 0.275x + 0.32$. Comparisons of slopes in PAST showed that they were significantly different ($p < .0002$).

synonym because the type material (Hall, 1863) includes both cranidia and a pygidium (e.g., Westrop, 1986, pl. 14, figs. 1, 2).

Although pygidia of typical species of Eurekiidae, including those of *Eureka* Walcott, 1916 and *Corbinia* Walcott, 1924, possess as many as six pairs of marginal spines and well-defined pleural furrows (e.g., Adrain and Westrop, 2004, pl. 12, pl. 13, figs. 18–20; Westrop et al., 2005, figs. 2.10–2.12, 8.1–8.3, 8.6–8.10), *Wisarcadiaspis* Westrop and Palmer, 2009 is much closer to *Monocheilus*. Although more convex than *Monocheilus*, the pygidium has an aspinose margin and weak pleural furrows (Westrop et al., 2005, fig. 6). The axis terminates well short of the posterior margin, and like *Monocheilus* (e.g., Westrop, 1986, pl. 15, fig. 4), it is composed of at least three segments, with two typically incorporated into the terminal piece. Thus, the presence of only a single pair of marginal spines in some species of *Monocheilus* is not a barrier to a phylogenetic relationship with other species of Eurekiidae.

Unlike typical Eurekiidae, the anterior border of *Monocheilus* lacks independent convexity, but the backwardly bowed border furrow (e.g., Figs. 2.2, 2.6, 2.11, 2.12, 3.6, 3.9; Westrop, 1986, pl. 15, figs. 7, 8) is similar to those in some species of *Corbinia* (e.g., Adrain and Westrop, 2004, pl. 13, figs. 2, 13; Westrop et al., 2005, fig. 7) and *Wisarcadiaspis* (e.g., Westrop et al., 2005, fig. 4). Effacement of the anterior border and border furrow, which occurs later in ontogeny (e.g., Figs. 3.1, 3.2, 6.1–6.3; Westrop, 1986, pl. 15, figs. 1, 2), is matched in “*Bayfieldia*” *simata* Winston and Nicholls, 1967 (pl. 9, figs. 20, 25). Moreover, the long genal spine of *Monocheilus* (e.g., Westrop, 1986, pl. 15, fig. 9), which contrasts with the miniscule spines of typical eurekiid librigenae (e.g., Westrop et al., 2005, fig. 8.4, 8.5), is also a feature of *Wisarcadiaspis*.

There are enough similarities in characters to provisionally view *Monocheilus* as a basal member of Eurekiidae. Further evaluation of this hypothesis must await a computer-based phylogenetic analysis of Eurekiidae that will also need to include a revision of “*Bayfieldia*” *simata* Winston and Nicholls,

1967 (including their “var. A,” which represents a distinct species), which combines a *Monocheilus*-like cranium with a conventional eurekiid pygidium that includes five to six pairs of marginal spines and well-furrowed pleural fields (e.g., Winston and Nicholls, 1967, pl. 9, figs. 20, 23–26).

Genus *Monocheilus* Resser, 1937

Type species.—*Conocephalites anatinus* Hall, 1863 from the Lone Rock Formation, Wisconsin (by original designation).

Diagnosis.—Eurekiidae with preglabellar field of cranium separated from anterior border by weak, backwardly curved anterior border furrow in small cranidia that becomes effaced in larger holaspids, producing an undifferentiated frontal area. Glabella parallel-sided to gently tapered anteriorly with very weakly incised glabellar furrows barely perceptible in larger holaspids. Transversely subelliptical pygidium bearing one to four pairs of short, triangular marginal spines. Short, convex axis consists of one axial ring and terminal piece composed of at least two segments. Pygidial pleural field is nearly flat.

Remarks.—Previous authors (e.g., Grant, 1962; Westrop, 1986) have treated *Monocheilus* and *Stigmacephalus* as distinct genera. *Monocheilus reginae* n. sp. (Figs. 2, 3) and *M. richardi* n. sp. (Figs. 5, 6) from the uppermost Honey Creek Formation are clearly related to the type species of *Stigmacephalus*, *S. oweni* (Hall, 1863), and provide new information on the librigena and pygidium. They also provide character support for synonymy of *Monocheilus* and *Stigmacephalus*. Cranidia of *M. reginae* and *M. richardi* differ in the size of the palpebral lobes, with the relatively long-eyed *M. reginae* resembling such species as *M. micros* (Walter, 1924) (Westrop, 1986, pl. 15, figs. 1–3, 5, 6). By contrast, *M. richardi* has smaller palpebral lobes that are comparable to *S. oweni* (e.g., Nelson, 1951, pl. 109, figs. 1, 2; Westrop, 1986, pl. 15, figs. 10, 11). As such, *M. reginae* and *M. richardi* bridge the cranial morphologies of *Monocheilus* and *Stigmacephalus*.

As will be discussed, there appear to be two pygidial morphotypes associated with cranidia of *M. reginae* and *M. richardi* in BM 79.4T that differ in outline (Fig. 7.1–7.5 and Fig. 7.6, 7.7, respectively; species assignments are uncertain), and both are very similar to those of *M. anatinus* (Hall, 1863; Bell et al., 1952, pl. 33, fig. 5a; Westrop, 1986, pl. 14, fig. 3) and *M. micros* (Walter, 1924; Westrop, 1986, pl. 15, fig. 4). In particular, all of these pygidia share triangular spines on the posterior corners and a single pair of broad, shallow pleural furrows on a relatively flat pleural field. The axis is short, occupying about half of pygidial length, with one well-defined axial ring and a second ring that is partly fused with the terminal piece. They lack a border and border furrow. All are distinct from the specimen attributed to *S. oweni* by Nelson (1951, pl. 109, fig. 9), which has a long axis that terminates close to the pygidial margin, a narrow border, and distinct border furrow and lacks marginal spines. It is almost certainly misassigned, and consequently, use of pygidial characters to separate *Monocheilus* and *Stigmacephalus* (e.g., Westrop, 1986, p. 87) can no longer be justified.

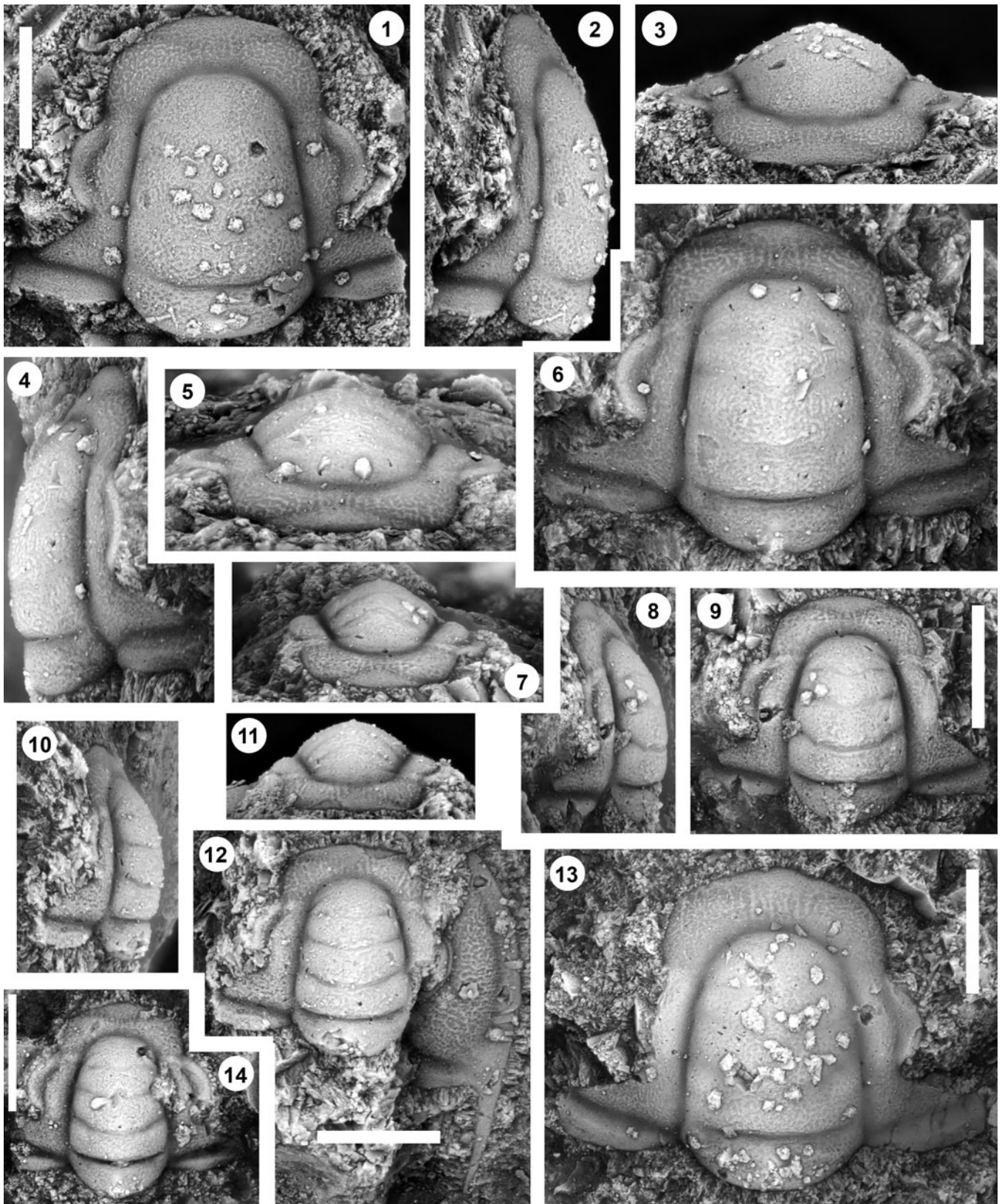


Figure 5. *Monocheilus richardi* n. sp. from the uppermost Honey Creek Formation, Bally Mountain section, Kiowa County, Oklahoma. All are cranidia from collection BM 79.4T. All are paratypes. (1–3) OU 238366: (1) dorsal view; (2) lateral view; (3) anterior view. (4–6) OU 238163: (4) lateral view; (5) anterior view; (6) dorsal view. (7–9) OU 238367: (7) anterior view; (8) lateral view; (9) dorsal view. (10–12) OU 238368a: (10) lateral view; (11) anterior view; (12) dorsal view (associated free cheek, OU 238368b, is visible). (13) OU 238369, dorsal view. (14) OU 238370, dorsal view. Scale bars = 1 mm.

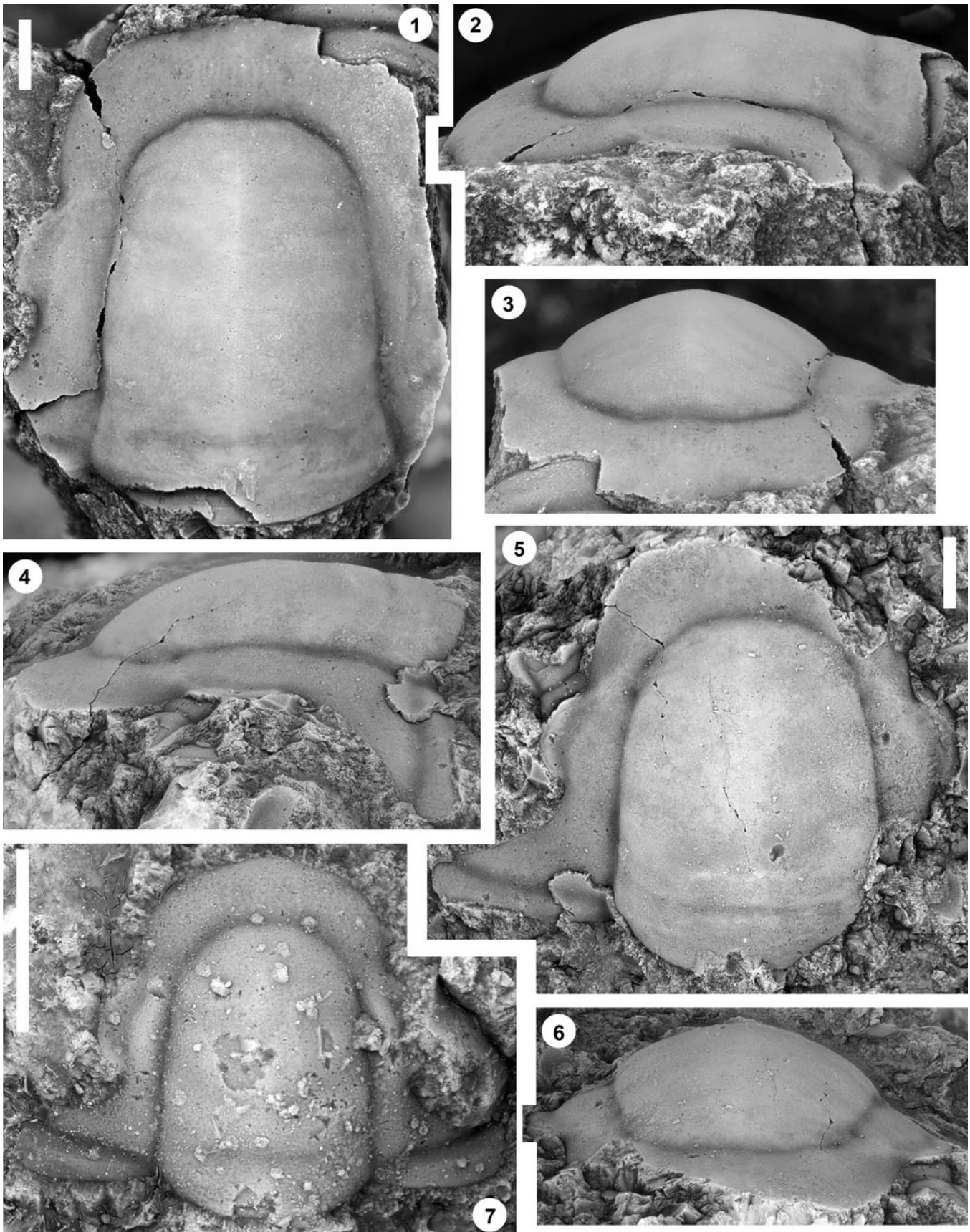


Figure 6. *Monocheilus richardi* n. sp. from the uppermost Honey Creek Formation, Bally Mountain section, Kiowa County, Oklahoma. All are cranidia from collection BM 79.4T. (1–3) Paratype OU 238371: (1) dorsal view; (2) lateral view; (3) anterior view. (4–6) Holotype OU 238372: (4) lateral view; (5) dorsal view; (6) anterior view. (7) Paratype OU 238373, dorsal view. Scale bars = 2 mm.

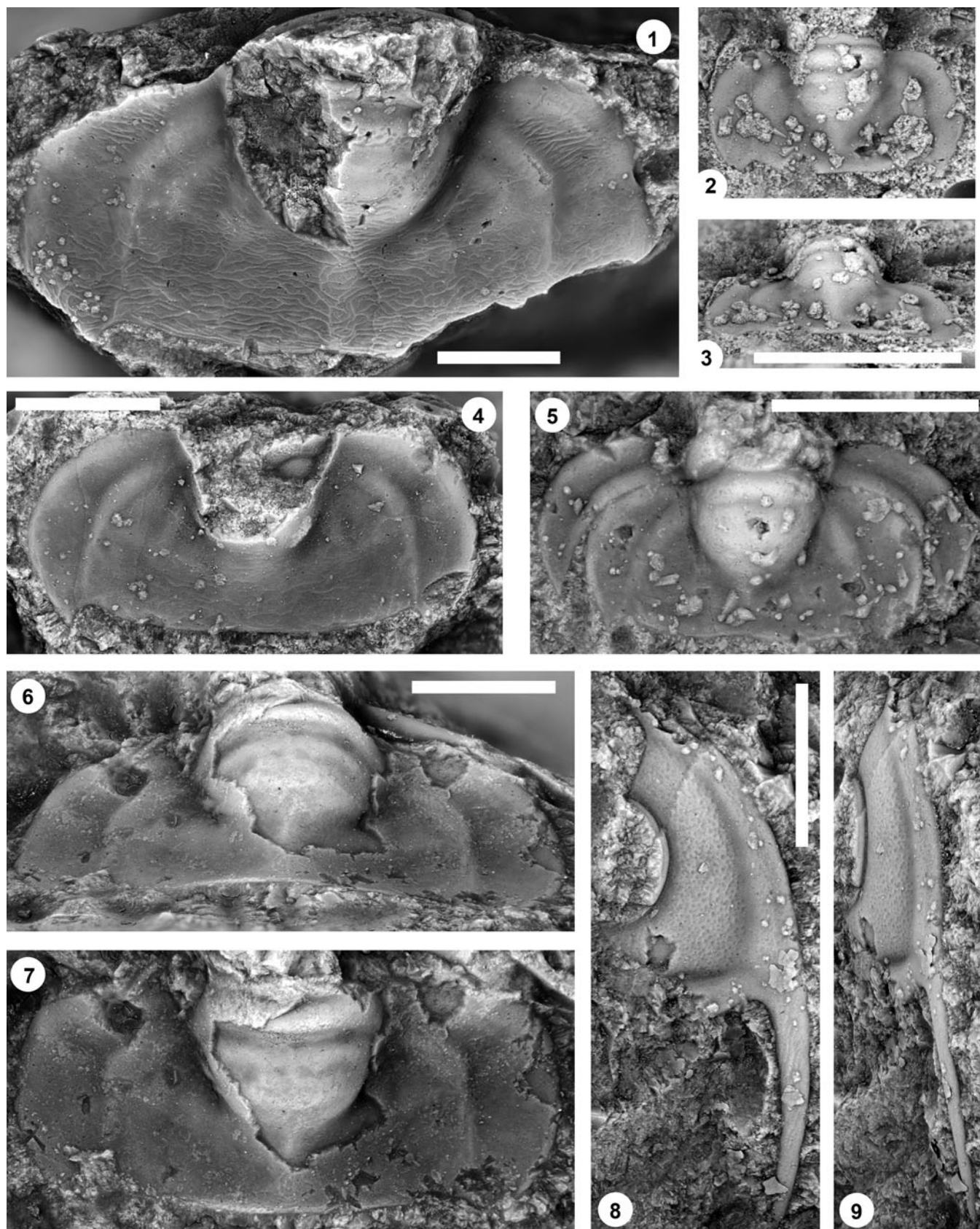


Figure 7. (1–7) *Monocheilus* spp. from the uppermost Honey Creek Formation, Bally Mountain section, Kiowa County, Oklahoma. All are pygidia from collection BM 79.4T. (1) OU 238374, dorsal view. (2, 3) OU 238375: (2) dorsal view; (3) posterior view. (4) OU 238162, dorsal view. (5) OU 238376, dorsal view. (6, 7) OU 238161: (6) posterior view; (7) dorsal view. (8, 9) *Monocheilus reginae* n. sp. from collection BM 79.4T, librigena, OU 238377: (8) dorsal view; (9) lateral view. Scale bars = 2 mm.

Librigenae of *M. micros* (e.g., Bell et al., 1952, pl. 33, fig. 4a; Westrop, 1986, pl. 15, fig. 9) and *M. reginae* (Fig. 7.8, 7.9) are very similar, with long genal spines, and are separable only on the basis of sculpture: the former has a smooth external surface, like the rest of the cephalon, whereas the latter is pitted. Aside from sculpture, cranidia of these two species are differentiated primarily on the position of the palpebral lobe. *Monocheilus reginae* resembles *S. oweni* (e.g., Westrop, 1986, pl. 15, figs. 11, 13) in possessing a palpebral lobe that is separated from the glabella both anteriorly and posteriorly by a distinct, continuous band of fixigena (Figs. 2, 3), as does *M. richardi* (Figs. 5, 6). By contrast, larger cranidia of *M. micros* (e.g., Bell et al., 1952, pl. 33, fig. 4b; Westrop, 1986, pl. 15, fig. 1) have palpebral lobes that are located closer to the glabella so that the palpebral furrows and axial furrows merge anteriorly, and only the posterior tip of the lobe is separated by a narrow strip of fixigena; similar palpebral lobe positions characterize *M. anatinus* (e.g., Bell et al., 1952, pl. 33, fig. 5c, pl. 34, fig. 2; Westrop, 1986, pl. 14, fig. 1), *M. truncatus* Ellinwood in Bell and Ellinwood, 1962 (e.g., Westrop, 1986, pl. 14, figs. 3–5), and *M. orestes* Westrop, 1986 (pl. 15, figs. 14–17). However, small cranidia of *M. micros* clearly have palpebral lobes that are farther from the glabella (Westrop, 1986, pl. 15, fig. 7), resembling the condition in *M. reginae* and *M. richardi*, and the palpebral lobe shifts toward the glabella during holaspid ontogeny. The polarity of ontogenetic change indicates that a palpebral lobe and, therefore, eyes that are located close to the glabella represent the apomorphic condition. This is also supported by potential outgroups such as *Minkella* (e.g., Westrop, 1986, pl. 14, figs. 7–16), in which the palpebral lobe is separated from the glabella by a broad, continuous band of fixigena. *Stigmacephalus* appears to rest only on the retention of this plesiomorphic character state, and recognition of *Monocheilus* on the basis of a palpebral lobe that abuts the glabella likely makes *Stigmacephalus* paraphyletic. *Stigmacephalus* is therefore treated as a junior synonym of *Monocheilus*. As revised here, *Monocheilus* includes, at minimum, *M. anatinus*, *M. oweni*, *M. oweni* var. A of Nelson, 1951 (which represents a distinct species; see Westrop, 1986, p. 89), *M. micros*, *M. truncatus*, *M. orestes*, *M. reginae*, and *M. richardi*. Pygidial characters, including the relatively flat pleural field, short axis, and triangular marginal spines (up to four pairs; Westrop, 1986, pl. 14, fig. 6; Stitt and Straatmann, 1997, fig. 8.14), are potential apomorphic characters supporting monophyly. Effacement of the anterior border and border furrow is shared with species such as “*Bayfieldia*” *simata* Winston and Nicholls, 1967. The differences in pygidial anatomy between “*B.*” *simata* (e.g., Winston and Nicholls, 1967, pl. 9, fig. 23) and *Monocheilus* (e.g., Fig. 7.1–7.7) raise the possibility that similarities in frontal area anatomy are homoplastic, in which case effacement would be another character supporting monophyly of the latter.

Monocheilus reginae new species
Figures 2, 3, 7.8, 7.9

Holotype.—A cranidium (Fig. 3.5–3.7; OU 238158) from the Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T.

Paratypes.—Eleven cranidia (OU 238164, OU 238356–OU 238365) and one librigena (OU 238377), all from the Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T.

Diagnosis.—*Monocheilus* with large palpebral lobe about 60% (59%; 42%–64%; lower values in larger specimens [e.g., Fig. 3.1]) of preoccipital glabellar length; both anterior and posterior ends separated from glabella by narrow strips of fixigena. Faint anterior border furrow curved backward; anterior border roughly rhombic in outline. Pitted sculpture with pitted sculpture augmented by caecal network on frontal area that is best expressed on smaller specimens (e.g., Fig. 2.9, 2.10) and faint to absent on anterior border.

Occurrence.—Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collections BM 79.4T and BM 80.7, *Monocheilus reginae* fauna.

Description.—Cranidium exclusive of posterolateral projection subrectangular in outline with gently rounded anterior margin; width across palpebral lobes equal to length (101%; 98%–103%). Axial and preglabellar furrows finely etched grooves. Glabella conspicuous, accounting for about 81% (79%–83%) of cranial length and about 65% (57%–70%; lower values in smaller cranidia) of cranial width, and gently convex; weakly tapered, with anterior margin rounded. Occipital furrow (SO) shallow, curved gently backward, terminating short of axial furrow. Occipital ring (LO) occupies about one-fifth (21%; 19–23%) of glabellar length. Short anterior border expressed on some specimens but not elevated above adjacent part of preglabellar field; border furrow faint and curved backward. Palpebral lobe forms nearly flat, arcuate band centered in front of glabellar mid-length, length about 60% (59%; 42%–64%; lower values in larger specimens) of preoccipital glabellar length; palpebral furrow lightly impressed curved groove. Narrow palpebral area accounts for about 26% (21%–35%; higher values in smaller specimens) of glabellar width opposite midpoint of palpebral lobe. Anterior branches of facial sutures nearly parallel before curving inward along anterior cranial margin; posterior branches diverge backward in faintly sigmoid curve. Posterior border convex, expands abaxially, with maximum length (exsagittal [exsag.]) equal to 14% (12%–15%) of glabellar length; posterior border furrow is clearly defined groove directed obliquely forward from axial furrow. Sculpture of irregular pits on external surface except for furrows and palpebral lobes; overprinted with caecal network on preglabellar field that becomes faint to absent on anterior border.

Librigena with long genal spine. Librigenal field well inflated; carries same pitted sculpture as the cranidium, which also extends to the anterior sections of the librigenal border. Librigenal border furrow weakly impressed; border gently convex. Faint terrace ridges on posterior librigenal border and genal spine.

Etymology.—For Regina Blackwell, Sean Blackwell’s mother.

Additional material.—In addition to the types, six cranidia were complete enough to provide morphometric data.

Ontogeny.—Small cranidia (e.g., Fig. 2.6, 2.12) have a roughly rhombic anterior border and backwardly curved border furrow (small cranidia of *M. micros* are similar in this respect [Westrop, 1986, pl. 15, figs. 7, 8]). The border furrow is lost in larger specimens, but the border may be identifiable by a change in surface sculpture on the frontal area from caecal markings to a more pitted surface (Figs. 2.9, 3.6). However, although the frontal area in smaller specimens (e.g., Fig. 2.12, 2.14) includes caecal ridges, they fade in larger specimens (e.g., Fig. 3.4) so that the border is more difficult to identify. The palpebral lobe becomes shorter, with length dropping from about 60% of preoccipital glabellar length in smallest specimens (e.g., Fig. 2.6, 2.11, 2.12, 2.13) to slightly more than 40% in the largest (e.g., Fig. 3.1). Glabellar furrows also exhibit ontogenetic variation. Smaller specimens have finely etched, transglabellar S1 and S2 furrows and faint S3 lateral furrows, and SO extends across the entire width of the glabella (e.g., Fig. 2.6, 2.11). SO is expressed in larger specimens but becomes shallower and terminates short of the lateral glabellar margin (e.g., Figs. 2.1, 3.4, 3.6). Other glabellar furrows become faint (e.g., Fig. 2.13) and are eventually lost entirely (e.g., Fig. 3.4), even on internal molds (e.g., Fig. 3.1).

Remarks.—A comparison between cranidia of *M. reginae* and *M. richardi*, co-occurring species that differ in the size of the palpebral lobe (Fig. 4), is presented in the description of the latter. There appear to be two distinct pygidial morphotypes associated with the cranidia, raising the possibility that other characters may separate these species. However, more material is needed to confirm this. The most common morphotype (e.g., Fig. 7.1–7.5) is relatively long and narrow, with length (measured to the intersection of the anterior margin and the axis) equal to 46% of width, but one specimen (Fig. 7.6, 7.7) is distinctly shorter and wider, with length equal to 40% of width.

Among other species, *M. reginae* is similar to sclerites from the Bison Creek Formation, southern Alberta, that were assigned to *M. micros* (Walter, 1924) by Westrop (1986, pl. 15, figs. 1–9). As noted earlier, free cheeks can be distinguished only on the basis of sculpture (smooth in *M. micros* and pits on *M. reginae*; a difference that extends to the cranidia). The position of the palpebral lobe is also diagnostic; it is much closer to the axial furrow in *M. micros*, particularly at the anterior tip (compare Figs. 2, 3 with Westrop, 1986, pl. 15, figs. 1, 2). A consequence of this position in *M. micros* is a relatively narrower (transverse [tr.] frontal area that is also longer than in *M. reginae*. *Monocheilus anatinus* (Hall, 1863) (e.g., Westrop, 1986, pl. 14, fig. 1), *M. truncatus* Ellinwood in Bell and Ellinwood, 1962 (e.g., Westrop, 1986, pl. 14, figs. 3, 4), and *M. orestes* Westrop, 1986 (pl. 15, figs. 14–17) also differ from *M. reginae* in having larger palpebral lobes that are much closer to the glabella.

Monocheilus richardi new species
Figures 5, 6

Holotype.—A cranidium (Fig. 3.5–3.7, OU 238158) from the Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T.

Paratypes.—Nine cranidia (OU 238163, OU 238366, OU 238367, OU 238368a, OU 238369–OU 238373) and a librigena (OU 238368b) from the Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T.

Diagnosis.—*Monocheilus* with small palpebral lobe slightly more than 40% (42%; 30%–50%; lower values in larger specimens [e.g., Fig. 6.5]) of preoccipital glabellar length; both anterior and posterior ends separated from glabella by narrow strips of fixigenae. Faint anterior border furrow expressed on smaller specimens, curved backward; anterior border roughly rhombic in outline. Cephalon with pitted sculpture augmented by caecal network that is best expressed on smaller specimens (e.g., Fig. 5.1).

Occurrence.—Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collections BM 79.4T and BM 80.7, *Monocheilus reginae* fauna.

Description.—*Monocheilus richardi* is sufficiently similar to *M. reginae* that a comparison can be presented instead of a full description. *Monocheilus reginae* differs from co-occurring cranidia of *M. richardi* in the size of the palpebral lobe (Fig. 4). Compared with *M. richardi* (Figs. 5, 6), *M. reginae* is a relatively large-eyed species with a palpebral lobe that is equal to about 60% (59%; 42%–64%; lower values in larger specimens) of preoccipital glabellar length, whereas the palpebral lobe is noticeably smaller in similarly sized specimens of *M. richardi*, averaging slightly more than 40% (42%; 30%–50%; lower values in larger specimens). In other respects, the cranidia are similar.

Etymology.—For Richard Blackwell, the name of both Sean Blackwell's father and Sean Blackwell's grandfather.

Additional material.—In addition to the types, three cranidia were complete enough to provide morphometric data.

Remarks.—As in *Monocheilus reginae*, the palpebral lobe of *M. richardi* becomes proportionately smaller during ontogeny. However, the palpebral lobe of *M. richardi* is relatively smaller throughout growth (Fig. 4). In smaller specimens of *M. richardi* (e.g., Fig. 5.1–5.13), the palpebral lobe is 44% (42%–50%) of preoccipital glabellar length, well below the values (61%; 56%–64%) of similarly sized *M. reginae* (e.g., Fig. 2) and in fact similar to the proportions of the largest cranidia of *M. reginae* (42%).

The pitted sculpture is a diagnostic feature of both *M. reginae* and *M. richardi*, whereas other species, including *M. micros* and *M. orestes*, are smooth (e.g., Westrop, 1986, pl. 15, figs. 5, 6, 14, 15). Cranidia of *M. richardi* are similar to the types and other specimens of *M. oweni* (Hall, 1863) from the Upper Mississippi Valley region (e.g., Nelson, 1951, pl. 109, figs. 1, 2) in possessing a relatively small palpebral lobe, although *M. richardi*

differs in having a wider palpebral area of the fixigena so that the palpebral lobe is farther from the glabella. Unfortunately, all of the specimens from the Upper Mississippi Valley are preserved as sandstone internal molds, and the nature of the sculpture cannot be determined. It is impossible to compare *M. oweni* completely with other species that preserve the skeleton. As noted earlier, we recommend that the name *M. oweni* be restricted to the types, and the shutter-mark convention (*M. "oweni"*) should be used for internal molds from other collections in the Upper Mississippi Valley, as well as for specimens attributed to this species from Alberta (Westrop, 1986, pl. 15, figs. 10–13).

Monocheilus spp.
Figures 7.1–7.7, 8

Occurrence.—Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collections BM 79.4T and BM 80.7, *Monocheilus reginae* fauna.

Remarks.—*Monocheilus reginae* and *M. richardi* are differentiated clearly by the sizes of their palpebral lobes. As noted in the preceding, there is sufficient variation in pygidia from collection BM 79.4T that we anticipate larger samples will demonstrate that these species are also differentiated by pygidial anatomy, although the correct sclerite associations cannot be made at present. Pygidial morphotypes are separated by their outlines. Most are relatively long and narrow (e.g., Fig. 7.1–7.5), with length (measured to the intersection of the anterior margin and the axis) equal to 46% of width. The other pygidial morphotype (Fig. 7.6, 7.7) is relatively shorter and wider, with length equal to 40% of width, and has less strongly curved lateral margins. In other respects, the morphotypes are similar, with a single pair of triangular marginal spines. The axis is short with one distinct axial ring bounded posteriorly by a complete ring

furrow, and the terminal piece comprises at least two segments. The pleural field is nearly flat and crossed by a single pair of wide, shallow pleural furrows that curve sharply backward, separating narrow, convex anterior and posterior pleural bands.

Associated thoracic segments (Figs. 7.5, 8.2–8.5) have short (tr.) pleurae with well-defined, broad pleural furrows. The posteriormost segment is curved strongly backward (Fig. 7.5), but other specimens have transverse pleurae and were presumably positioned farther forward in the thorax (e.g., Fig. 8.4).

Family Ptychaspidae Raymond, 1924
Genus *Ptychaspis* Hall, 1863

Type species.—*Dikelocephalus miniscaensis* Owen, 1852 from the Lone Rock Formation, Minnesota (subsequent designation by Miller, 1889; see Bell et al., 1952).

Ptychaspis bullasa Lochman and Hu, 1959
Figures 9–12

- 1959 *Ptychaspis bullasa* Lochman and Hu, p. 422, pl. 58, figs. 21–42.
non 1962 *Ptychaspis bullasa*; Bell and Ellinwood, p. 405, pl. 58, figs. 14–17 [= *Ptychaspis occulta* n. sp.].
non 1970 *Ptychaspis bullasa*; Longacre, p. 44, pl. 2, figs. 4, 5 [= *Ptychaspis* spp.].
1971 *Ptychaspis bullasa*; Hu, p. 97, pl. 17, figs. 1–34; text-fig. 46.
non 1977 *Ptychaspis bullasa*; Stitt, p. 43, pl. 2, fig. 4.
non 1986 *Ptychaspis bullasa*?; Westrop, pl. 8, figs. 9–12 [= *Ptychaspis* spp.].
non 1997 *Ptychaspis bullasa*; Stitt and Straatmann, p. 90, fig. 7.16 (= *Ptychaspis* sp. indet).

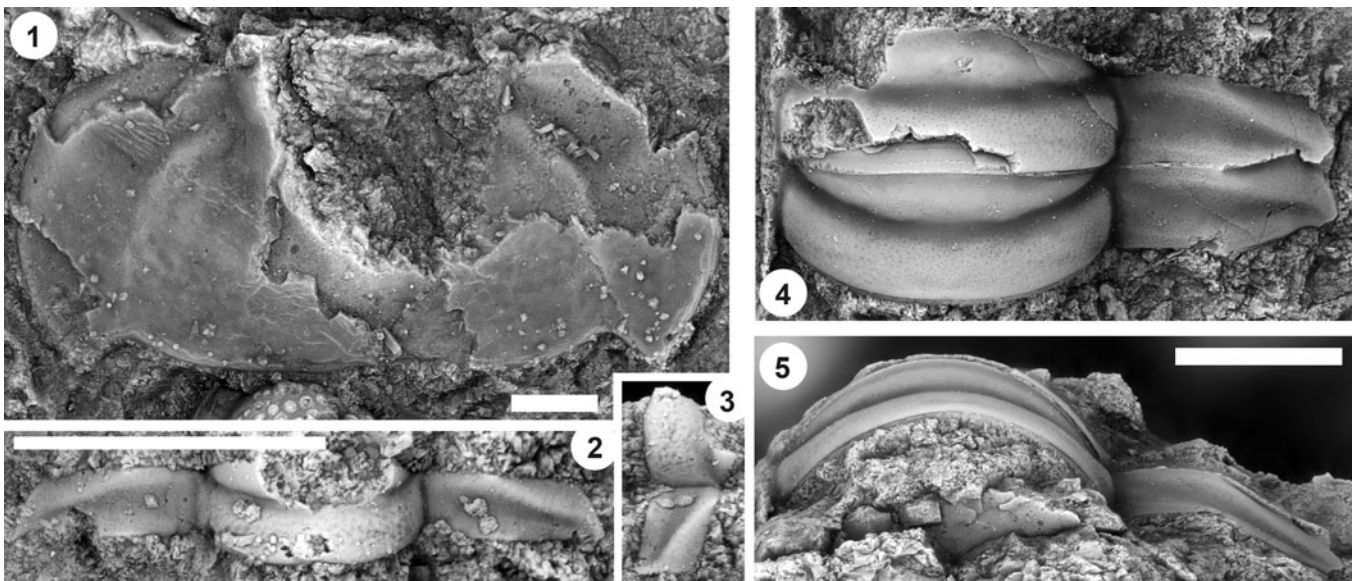


Figure 8. *Monocheilus* spp. from the uppermost Honey Creek Formation, Bally Mountain section, Kiowa County, Oklahoma. All are thoracic segments except for (1) (pygidium), and all are from collection BM 79.4T. (1) OU 238378, dorsal view. (2, 3) OU 238379: (2) dorsal view; (3) lateral view. (4, 5) OU 238380: (4) dorsal view; (5) posterior view. Scale bars = 2 mm.

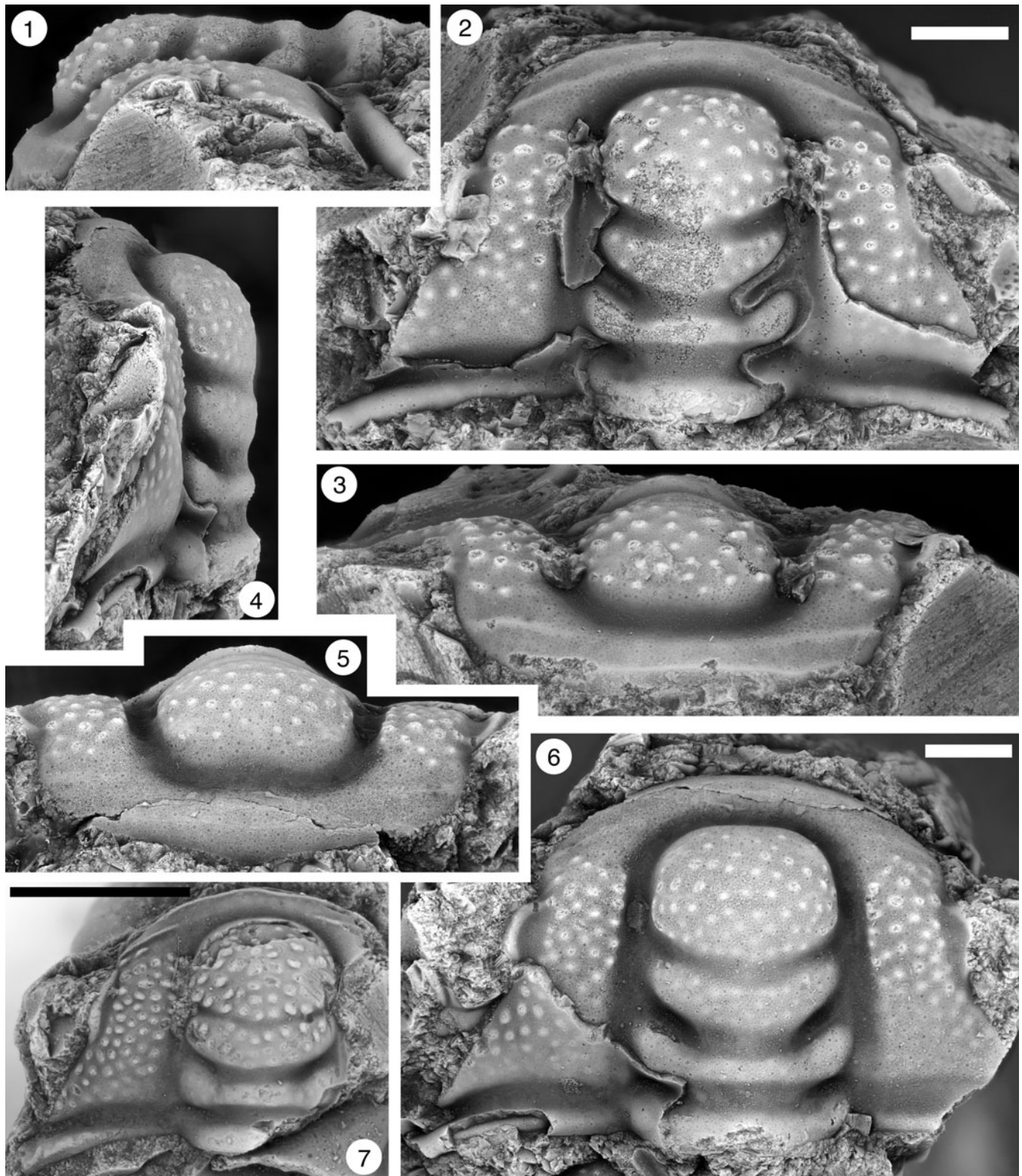


Figure 9. (1–6) *Ptychaspis bullasa* Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho. All are cranidia. (1–3) Holotype USNM 137099: (1) lateral view; (2) dorsal view; (3) anterior view (illustrated previously by Lochman and Hu, 1959, pl. 58, figs. 39, 40). (4–6) Paratype USNM 137100k: (4) lateral view; (5) anterior view; (6) dorsal view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 37). (7) USNM 137100, dorsal view (previously unfigured and not a designated paratype; see Lochman and Hu, 1959, p. 423 for the list of paratypes). Scale bars = 2 mm.

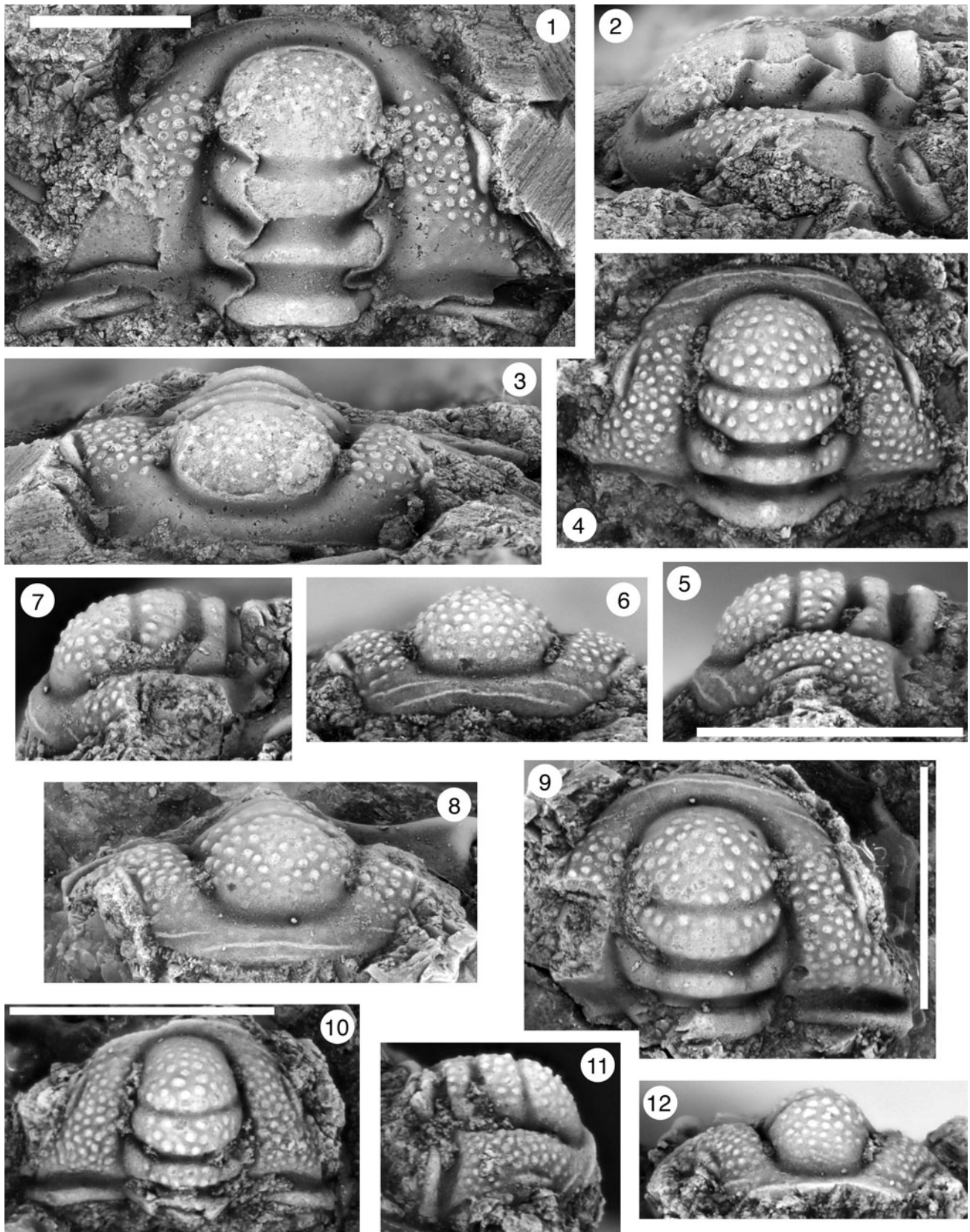


Figure 10. *Ptychaspis bullasa* Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho. All are cranidia and all paratypes. (1–3) USNM 135100c: (1) dorsal view; (2) lateral view; (3) anterior view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 35). (4–6) USNM 137100e: (4) dorsal view; (5) lateral view; (6) anterior view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 26). (7–9) USNM 137100d: (7) lateral view; (8) anterior view; (9) dorsal view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 24). (10–12) USNM 137100c: (10) dorsal view; (11) lateral view; (12) anterior view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 23). Scale bars = 2 mm.

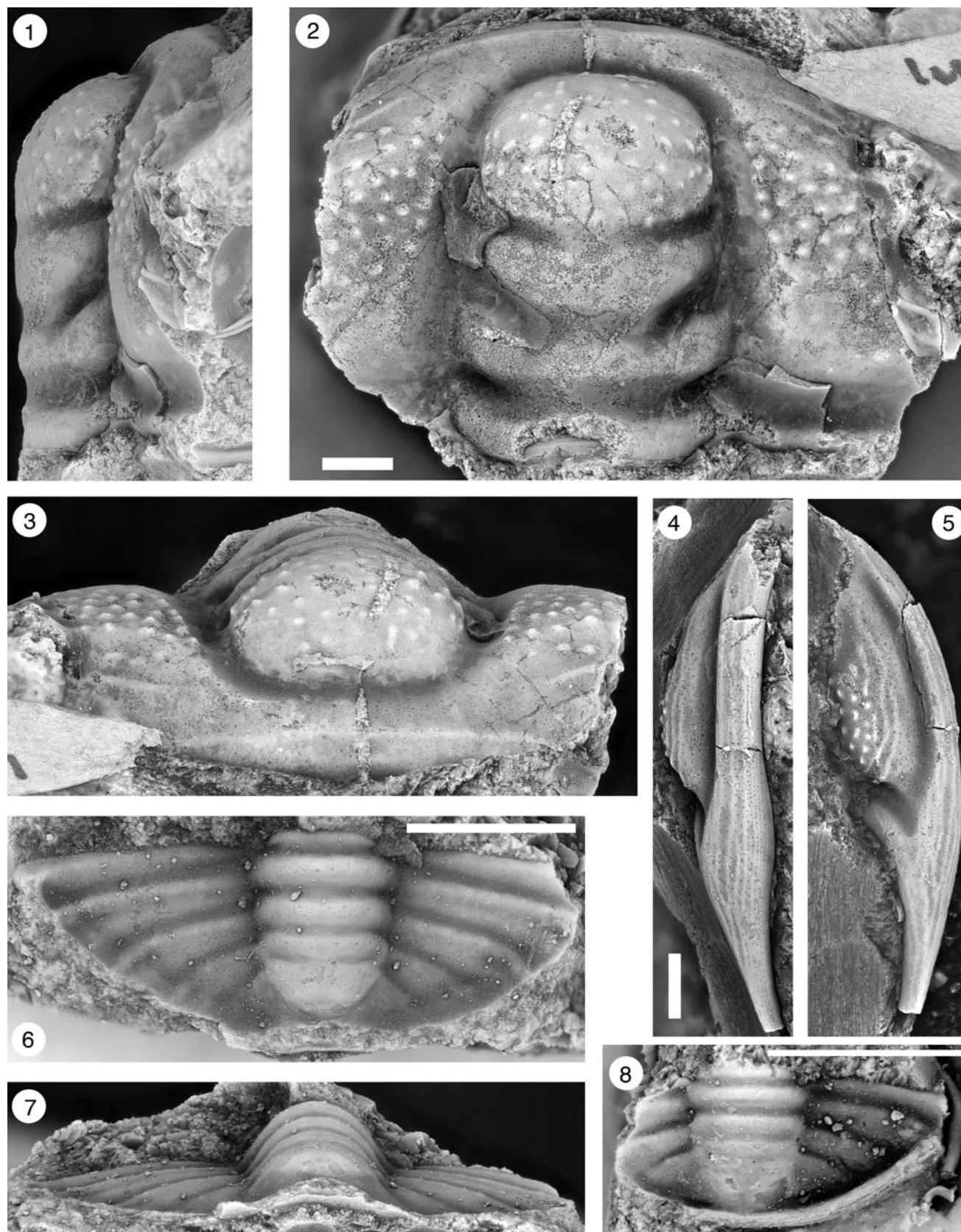


Figure 11. *Ptychaspis bullasa* Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho. All are paratypes. (1–3) Cranidium, USNM 137100n: (1) lateral view; (2) dorsal view; (3) anterior view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 42). (4, 5) Librigena, USNM 137100j: (4) lateral view; (5) dorsal view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 36). (6, 7) Pygidium, USNM 137100s: (6) dorsal view; (7) posterior view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 30). (8) Pygidium, USNM 137100p, dorsal view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 31). Scale bars = 2 mm.

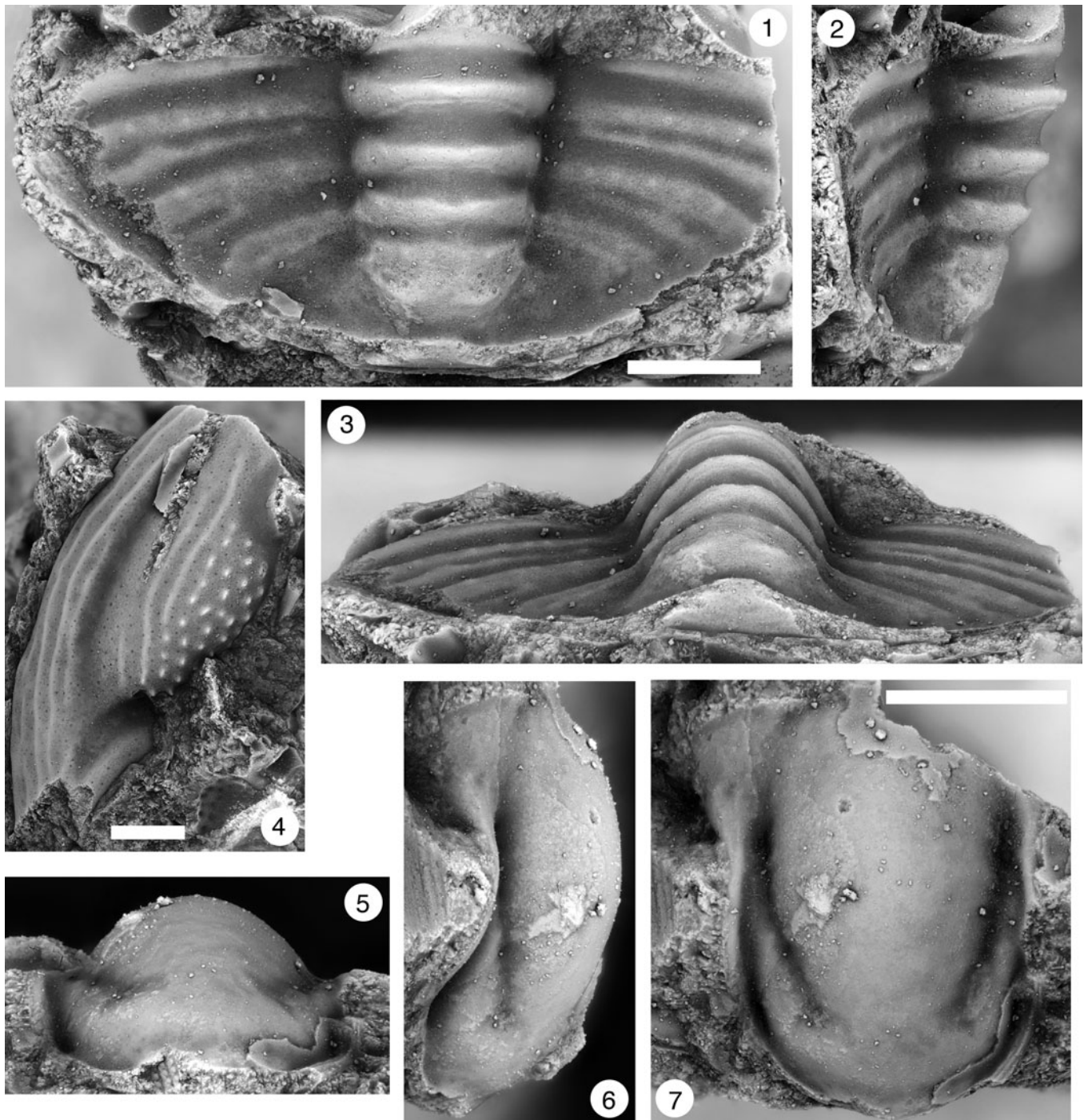


Figure 12. *Ptychaspis bullasa* Lochman and Hu, 1959, St. Charles Formation, Bear River Range, Mink Creek, southern Idaho. All are paratypes. (1–3) Pygidium, USNM 137100L: (1) dorsal view; (2) lateral view; (3) posterior view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 27). (4) *Librigena*, USNM 137100f, dorsal view (previously unfigured). (5–7) Hypostome, USNM 137100m: (5) posterior view; (6) lateral view; (7) ventral view (illustrated previously by Lochman and Hu, 1959, pl. 58, fig. 25). Scale bars = 2 mm.

Holotype.—A cranidium (USNM 137099) from the St. Charles Formation, Idaho (Fig. 9.1–9.3).

Diagnosis.—*Ptychaspis* with palpebral lobes short and narrow, with midpoint situated roughly opposite S2 glabellar furrow. Anterior cranial margin gently curved so that frontal area maintains nearly even width (sagittal [sag.], exsag.). Cranidial

sculpture of tubercles extends forward on fixigena to point near level of S3 (where expressed), and in smaller cranidia extends back to posterior border furrow (e.g., Fig. 10.4, 10.10); tubercles are lost on posterior fixigenae on larger specimens (e.g., Figs. 9.6, 10.1). Frontal area lacks tubercles and has up to two striate ridges running parallel to anterior cranial margin. Anteriorly, pygidial pleural and interpleural

furrows extend nearly transversely (10° – 15° from transverse plane) from axis before curving backward near pygidial margin.

Occurrence.—St. Charles Formation, ridge north of Mink Creek, near Preston, southern Idaho (Lochman and Hu, 1959).

Description.—Cranidium with length equal to 95% (90%–99%) of width. Frontal area is short and lacks border furrow. Anterior cranial margin gently curved medially so that frontal area maintains nearly even length (sag., exsag.) across most of width. Glabella convex, long, and broad, occupying 89% (87%–91%) of cranial length and half (50%; 47%–53%) of cranial width between palpebral furrows; glabellar width at S2 equal to 60% (56%–63%) of glabellar length. SO firmly impressed, nearly transverse. S1 and S2 deeply incised and connected across glabella. S1 transverse medially but deflected forward abaxially; S2 curved backward. LO occupies 13% (12%–14%) of glabellar length, transverse over most of width but curved forward near axial furrow. L1 accounts for 13% (12%–14%) of glabellar length (sag.), transverse medially, but curved sharply forward abaxially. L2 roughly trapezoidal in outline, with nearly transverse anterior margin; occupies about one-sixth (16%; 12%–20%; highest values in smallest cranidia) of glabellar length. S3 faint at best on larger cranidia (e.g., Fig. 11.1, 11.2), nearly transverse; not expressed on smaller individuals (e.g., Fig. 10). Consequently, L3 and L4 essentially undifferentiated, forming a suboval region equal to about 40% (42%; 40%–44%) of glabellar length. Palpebral lobe short, narrow band centered opposite S2; length equal to roughly one-quarter (23%; 19%–27%; lowest value in largest cranidium; Fig. 11.2) of glabellar length. Palpebral furrow firmly impressed, narrow groove. Palpebral area of fixigena very gently inflated, width equal to 41% (37%–48%; higher values in larger cranidia) of glabellar width at S2. Posterior branches of facial suture strongly divergent; anterior branches nearly parallel in front of palpebral lobe before swinging inward along anterior cranial margin. Posterior border furrow well incised; posterior border strongly convex. Cranial sculpture of tubercles extends forward to point just in front of anterior tip of palpebral lobe. On smaller cranidia, tubercles extend back to posterior border furrow (e.g., Fig. 10.4, 10.9, 10.10) but are lost on posterior fixigenae on larger specimens (e.g., Figs. 10.6, 11.2). Frontal area lacks tubercles and has up to two striate ridges running parallel to anterior cranial margin. Tubercles absent from the posterior border throughout holaspid ontogeny. Internal mold includes scattered fine pits on glabella and fixigenae.

Librigena with stout genal spine. Lateral border furrow is well defined and merges posteriorly with posterior border. Lateral border is narrow and descends steeply at cephalic margin. Libriginal field strongly inflated with shallow eye socle furrow and low eye socle. Borders, spine, and abaxial parts of libriginal field carry coarse striate ridges; adaxially, libriginal field with tubercles.

Hypostome with convex median body divided into short posterior lobe and much longer anterior lobe by oblique middle furrow that is effaced medially. Macula indistinct oval region on internal mold. Lateral and posterior border furrows form deep grooves; narrow, rim-like borders. Broad, triangular anterior

wing. Patches of exoskeleton preserve terrace ridges on lateral border and smooth surface on anterior lobe of median body; internal mold smooth.

Pygidium semielliptical in outline, wider than long. Axis convex, extending almost entire pygidial length and narrow, occupying less than a third of pygidial width; composed of three axial rings and terminal piece on largest specimen (Fig. 12.1–12.3). Articulating and axial ring furrows transverse and deep; posteriormost shallower than others on smaller specimens, so that third ring poorly differentiated from terminal piece. Articulating half ring very short, less than half length of first axial ring. Deep pleural and shallower interpleural furrows extend nearly transversely from axis at no more than 10° – 15° from transverse plane before curving backward more strongly near pygidial margin; posteriormost furrows more strongly deflected. Anterior pleural bands roughly equal to posterior bands. Posterior pleural bands carry row of faint tubercles. Pygidial border narrow, rising vertically from weakly convex pleural field.

Ontogeny.—Through the size range available for study (cranial lengths [sag.] from 1.5 to 15 mm), general cranial proportions show little change. For example, the glabella occupies between 87% and 91% of cranial length, and cranial length/width falls modestly from 96%–99% in cranidia less than 3 mm (sag.) to 91%–95% in cranidia between 10 and 11 mm (sag.). SO, S1, and S2 furrows become broader (sag., exsag.) through ontogeny, even allowing for differing expression between the external surface and internal molds. The palpebral lobe is noticeably smaller in the largest cranidium (Fig. 11.2; equal to 19% of glabellar length) and is proportionally larger in smaller specimens (e.g., Fig. 10.1, 10.4; 26%–27% of glabellar length). This change is accompanied by a widening of the palpebral area of the fixigena (equal to 37%–39% of glabellar width in Fig. 10.1, 10.4 but 48% of glabellar width in Fig. 11.2).

Pygidia are incomplete, but the smallest (Fig. 11.8) is relatively narrower (tr.) than in the other specimens (Figs. 11.6, 12.1), and the third axial ring is poorly defined. In all three specimens, the axis remains long and terminates close to the posterior border.

Remarks.—Restudy of the type material of *Ptychaspis bullasa* Lochman and Hu (1959; Figs. 9–12) shows that this species is characterized by an anteriorly positioned palpebral lobe that is centered opposite the S2 glabellar furrow, and pygidial pleural and interpleural furrows that are almost transverse over most of their widths. This allows several records of *P. bullasa* from outside the type area in southern Idaho (Figs. 13–17) to be evaluated critically.

Cranidia that Bell and Ellinwood (1962) identified as *P. bullasa* from the Morgan Creek Member of the Wilberns Formation, Texas (Fig. 15), have palpebral lobes that are larger and more posteriorly located (see also Longacre, 1970, p. 44) than those of the types (e.g., Figs. 9, 10). There are other differences in the cranidia from Texas, including a longer frontal area with subtriangular anterior cranial margin, more densely packed tuberculate sculpture, and striate ridges that are more closely spaced on the anterior border (Fig. 15). The Texas material is assigned to a new species, *P. occulta* (see the following).

However, the two cranidia from the Morgan Creek Member that Longacre (1970) assigned to *P. bullasa* (Fig. 17) are distinct from both *P. bullasa* and *P. occulta* (see discussion of *Ptychaspis* spp. that follows).

The cranidium attributed to *P. bullasa* by Stitt (1977, pl. 2, fig. 4) from the Fort Sill Formation of Oklahoma has been damaged since it was photographed and can no longer be evaluated fully. However, sclerites from the same stratigraphic interval in the lower Fort Sill Formation (Figs. 13, 14) represent a distinct species characterized by curved pleural and interpleural furrows on the pygidium, among other characters (see following discussion of *P. matuszaki* n. sp.).

The record of *P. bullasa* from the Deadwood Formation of South Dakota (Stitt and Straatmann (1997, fig. 7.16) is supported by a single illustrated librigena and is difficult to evaluate. This specimen has far greater development of striate ridges and a smaller area of tuberculate sculpture than either of the librigenae in the type lot of *P. bullasa* (Figs. 11.4, 11.5, 12.4), and the identification cannot be corroborated.

Finally, Westrop (1986, pl. 8, figs. 9–12) assigned sclerites from the Bison Creek Formation in the southern Canadian Rockies questionably to *P. bullasa*. The cranidia are from different localities and differ in details of the sculpture, with the larger specimen possessing highly irregular tubercles, some of which are connected by low ridges (Westrop, 1986, pl. 8, figs. 9, 10), whereas the smaller has rounded, isolated tubercles (Westrop, 1986, pl. 8, fig. 11). Tubercle shape is uniform through the holaspid ontogeny of *P. bullasa* (e.g., compare Fig. 10.4, 10.10 with Figs. 9.2, 9.6, 11.2), suggesting that the Bison Creek material records more than one species.

Rather than a single, widespread species, detailed comparisons of putative occurrences of *P. bullasa* indicate that there is in fact a geographically structured plexus of related species. Westrop et al. (2018) recently documented a similar pattern in the middle Cambrian trilobite *Eodiscus*, noting that such sets of pseudocryptic species are comparable to groups of modern species that are now recognized routinely in studies that integrate morphometric and genomic data.

Ptychaspis matuszaki new species
Figures 13, 14

1957 *Ptychaspis granulosa exsculpta* Frederickson and Matuszak in Matuszak [nomen nudum], p. 29, pl. 2, figs. 1–3.

Holotype.—A cranidium (OU 4268; Fig. 13.1–13.3) from the Fort Sill Formation, about 4.4 km southeast of Hennepin (SE Sec. 4, T1S, R1W), Murray County, Oklahoma.

Paratypes.—A cranidium (OU 238168; Fig. 14.1–14.3), two incomplete free cheeks (OU 238167, OU 4269; Figs. 13.4, 14.4, 14.5), and two pygidia (OU 4270, OU 238169; Figs. 13.5, 14.6, 14.7).

Diagnosis.—*Ptychaspis* with closely spaced tuberculate cephalic sculpture yielding to sparse striate ridges along cranial and librigenal margins. In front of transglabellar S2 furrow, glabella subcircular in outline, divided by barely perceptible S3 and S4 lateral furrows (most clearly visible in

lateral view; Fig. 13.2). Palpebral lobe small and located opposite S2. Gently convex baccula present on fixigena opposite L1 (arrow on Fig. 13.1). Pygidium possesses gently inflated pleural field and axis composed of three axial rings and terminal piece. Anteriorly, pleural and interpleural furrows deflected obliquely backward at angle of at least 20°–30° from transverse plane. Pygidial border forms narrow upturned rim that thickens toward axis.

Occurrence.—Fort Sill Formation, Oklahoma, 4.4 km southeast of Hennepin (SE Sec. 4, T1S, R1W), Murray County, Oklahoma. Matuszak (1957, p. 30) did not provide detailed stratigraphic occurrence data for *Ptychaspis* in the Fort Sill Formation, but he indicated that sclerites now assigned to *P. matuszaki* (Figs. 13.1–13.3, 13.5, 14.4, 14.5) occurred in the “basal Fort Sill Formation.”

Description.—Cranidium subtrapezoidal in outline with rounded anterior margin; short (tr.) posterolateral projections. Frontal area short, accounting for about 10% of cranial length, and slopes almost vertically forward. Anterior border furrow absent. Axial and preglabellar furrows firmly impressed grooves. Glabella well rounded anteriorly and inflated, comprising about 89% of cranial length and about 49% of cranial width. SO firmly impressed and of even incision across glabella; curved gently backward. LO occupies about 12% of glabellar length and curved forward abaxially; carries small median node on internal mold. S1 and S2 glabellar furrows connected across glabella. S1 nearly transverse medially but curves forward and deepens abaxially. L1 also curved forward and occupies about 10% of medial glabellar length. S2 shorter (sag., exsag.), shallower than S1, maintaining nearly even depth; less strongly curved. L2 accounts for about 17% of glabellar length medially but narrows slightly abaxially. S3 gently impressed, defined in part by break in sculpture, and nearly transverse. L3 and L4 similar in length (exsag.) to L2. Gently convex baccula present on fixigena opposite L1 (arrow on Fig. 13.1). Palpebral lobes incomplete, but palpebral furrows indicate that they are situated opposite S2. Palpebral area of fixigena equal to about 35% of glabellar width at S2. Anterior branches of facial suture converge forward in even curve. Posterior branches diverge gradually backward along a nearly straight path. Posterior border furrow deeply incised and broad with a narrow rim-like border. Surface sculpture uniformly tuberculate on L2, L3, and L4 but present only medially on L1; tubercles present on palpebral area and extend forward on preocular field to level of S3. On posterior area, tubercles confined largely to sutural margin. Internal mold includes scattered fine pits.

Free cheek with long, stout genal spine. Inflated librigenal field occupies 68% of width opposite eye; eye socle not preserved but eye socle furrow broad, shallow groove. Lateral border furrow well incised anteriorly but shallows near genal spine; lateral border narrow in dorsal view, descends nearly vertically from border furrow. Librigenal field with conspicuous tubercles that are lost near border furrow. Border with elongate, widely spaced striate ridges running parallel to lateral cranial margin.

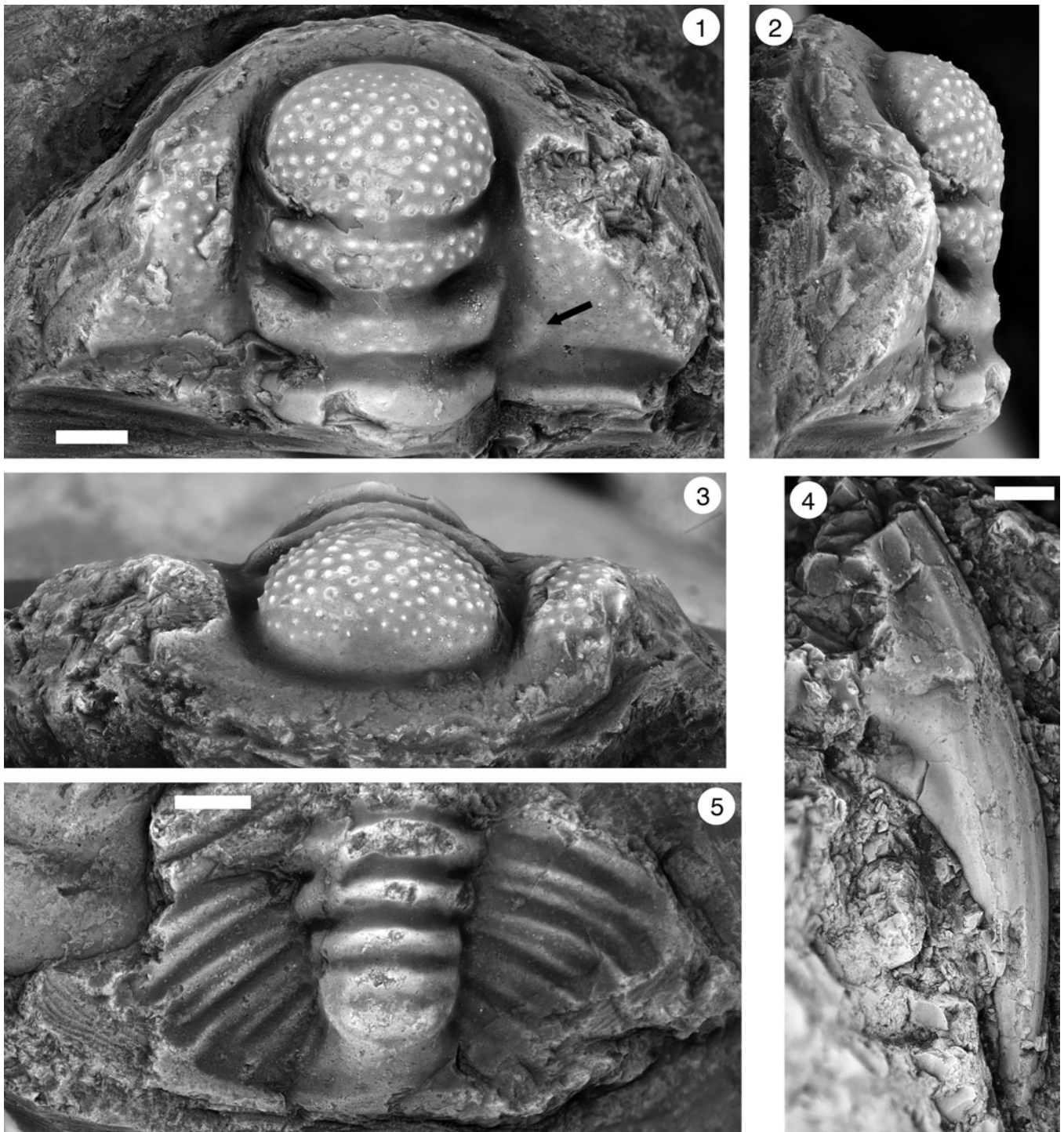


Figure 13. *Prychaspis matuszaki* n. sp., Fort Sill Formation, about 4.4 km southeast of Hennepin, Murray County, Oklahoma. (1–3) Holotype cranium, OU 4268: (1) dorsal view (note baccula, marked by arrow); (2) lateral view; (3) anterior view. (4) Paratype librigena, OU 238167, dorsal view. (5) Paratype pygidium, OU 4270, dorsal view. Scale bars = 2 mm.

Pygidium subelliptical in outline, width greater than length; gently arched in posterior view. Axis narrow, convex, occupies 67% of pygidial length. Three axial rings and terminal piece of at least two segments separated by well-defined, transverse ring furrows; shallower furrow present on terminal piece. Articulating half-ring short; articulating furrow nearly transverse. Pleural field crossed by at least four pairs of broad (exsag.), oblique

pleural furrows deflected backward at angle of at least 20°–30° from transverse plane; interpleural furrows narrower but well-defined grooves. Anterior and posterior pleural bands subequal, convex. Lateral and posterior borders form short (sag., exsag.), weakly upturned rim. External surface smooth; internal molds with pits; closely spaced on pleural field and border but widely spaced on crest of axis.

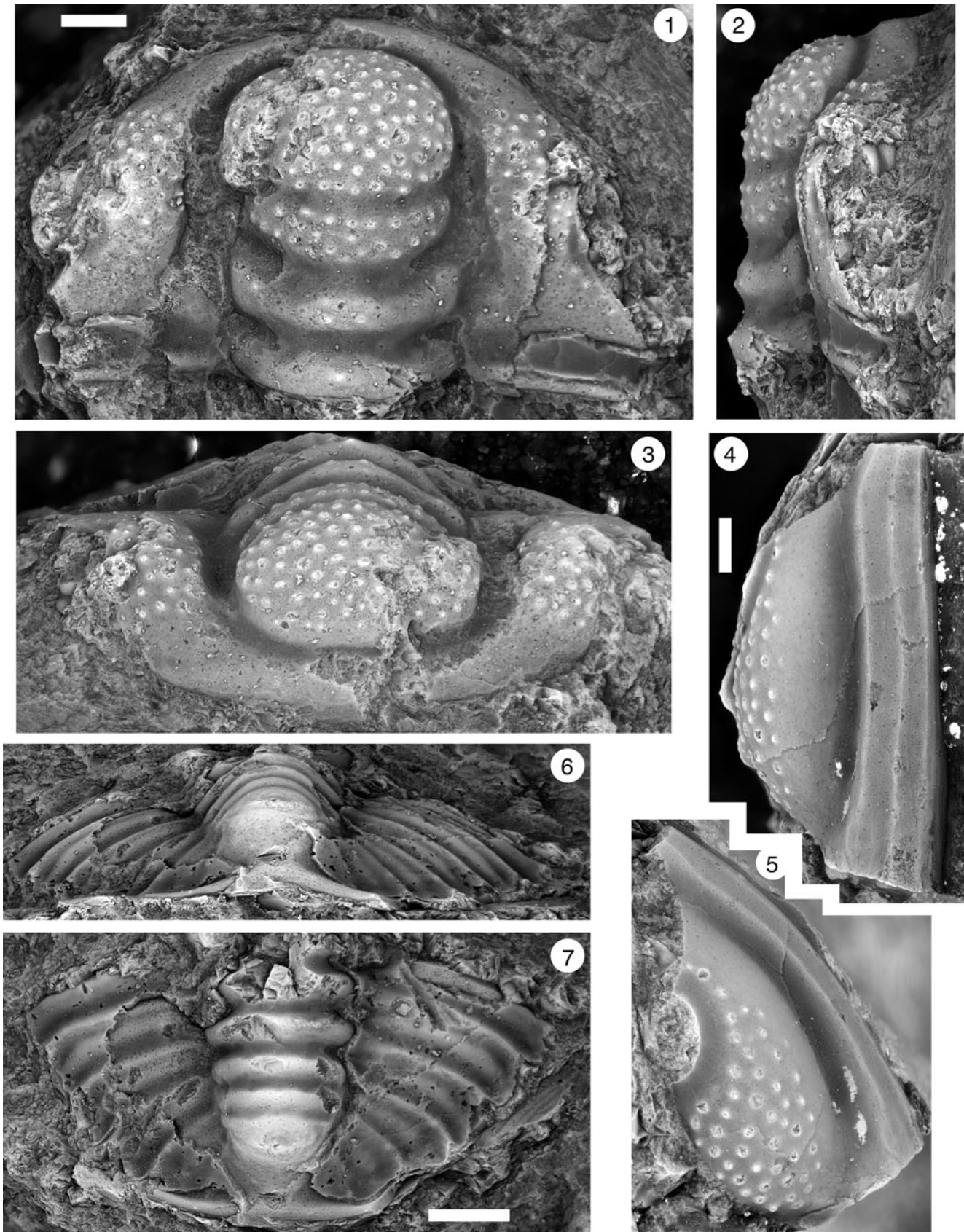


Figure 14. *Ptychaspis matuszaki* n. sp., Fort Sill Formation, about 4.4 km southeast of Hennepin (SE Sec. 4, T1S, R1W), Murray County, Oklahoma. All are paratypes. (1–3) Cranidium, OU 238168: (1) dorsal view; (2) lateral view; (3) anterior view. (4, 5) Librigena, OU 4269: (4) lateral view; (5) dorsal view. (6, 7) Pygidium, OU 238169: (6) posterior view; (7) dorsal view. Scale bars = 2 mm.

Etymology.—For David R. Matuszak, who recognized that this species was new in an unpublished thesis.

Remarks.—Crania of *Ptychaspis matuszaki* are similar to those of *Ptychaspis bullasa* Lochman and Hu, 1959 (Figs. 9–12). Both have tuberculate sculpture, but there are fewer, more widely spaced tubercles in *P. bullasa* (compare *P. matuszaki* [Figs. 13.1–13.3, 14.1–14.3] with *P. bullasa* [Figs. 9.1–9.3, 11.1–11.3]), which also has well-defined striate ridges on the frontal area. Both species have relatively small, anteriorly placed palpebral lobes that are centered near S2, and the overall proportions of the glabellar lobes are comparable. *Ptychaspis matuszaki* differs in having a distinct baccula next to L1 (seen most clearly in the best-preserved specimen; Fig. 13.1). In addition, cranidia of *P. bullasa* possess less rapidly diverging posterior suture branches, resulting in narrower (tr.) posterolateral projections. Pygidia share a raised, rim-like border, with those of *P. matuszaki* (e.g., Figs. 13.5, 14.6, 14.7) differing from *P. bullasa* (Figs. 11.6–11.8, 12.1–12.3) most clearly in having shorter axes and pleural and interpleural furrows that are deflected more strongly backward rather than being more transverse.

Crania of *P. striata* (Whitfield, 1878) and *Ptychaspis* cf. *P. miniscaensis* (Owen, 1852) from the Bison Creek Formation of Alberta (e.g., Westrop, 1986, pl. 8, figs. 1–3, 6, and pl. 7, figs. 1–4, respectively) are differentiated easily from *P. matuszaki* in having sculpture of coarse striate ridges that is expressed on both the external surface and the internal mold; tubercles are absent. In addition, the glabella of *Ptychaspis* cf. *P. miniscaensis* in front of S2 is tapered and subtrapezoidal, whereas the equivalent part of *P. matuszaki* is more rounded and subcircular in outline. S2 lateral furrows are connected across the glabella by a firmly impressed furrow in *P. matuszaki*, whereas S2 furrows are isolated to barely connected in *Ptychaspis* cf. *P. miniscaensis*. The raised, rim-like pygidial borders of both *P. matuszaki* and *Ptychaspis* cf. *P. miniscaensis* (e.g., Westrop, 1986, pl. 7, figs. 6, 11, 14) set them apart from *P. striata*, which has a flat pygidial border. *Ptychaspis* cf. *P. miniscaensis* has four axial rings in front of the terminal piece (e.g., Westrop, 1986, pl. 7, fig. 6), whereas *P. matuszaki* has only three (e.g., Fig. 13.5).

Ptychaspis miniscaensis is known only from sandstone internal molds from Lone Rock of Minnesota and Wisconsin (e.g., Bell et al., 1952, pl. 36, fig. 1a; Westrop, 1986, pl. 8, fig. 15) that are smooth or at best very weakly ridged even when well preserved. *Ptychaspis tuberosa* Feniak in Bell et al., 1952 (e.g., Westrop, 1986, pl. 8, fig. 14) also has a smooth internal mold.

Ptychaspis granulosa (Owen, 1852) is known only from poorly preserved sandstone internal molds from the Upper Mississippi Valley. Superficially, it is quite similar to *P. matuszaki* and *P. bullasa* in terms of tuberculate sculpture of the cranidium (e.g., Bell et al., 1952, pl. 34, fig. 6b, pl. 35, fig. 1a). However, the pygidial border in *P. granulosa* is broad and flat (e.g., Bell et al., 1952, pl. 35, figs. 1c, d) whereas the border of *P. matuszaki* is narrow and forms an upturned rim.

Ptychaspis occulta new species

Figure 15

1962 *Ptychaspis bullasa* Lochman and Hu; Bell and Ellinwood, p. 405, pl. 58, figs. 14–17.

Holotype.—A cranidium (USNM 185472; Fig. 15.6–15.8) from the Morgan Creek Member, Wilberns Formation, Little Llano River section, collection LL 725, San Saba County (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 16).

Paratypes.—Two cranidia (USNM 185437, 185470; Fig. 15.1–15.5) from the Morgan Creek Member, Wilberns Formation, central Texas.

Diagnosis.—A species of *Ptychaspis* with densely packed tuberculate cephalic sculpture on the postocular and palpebral areas and glabella yielding anteriorly to robust striate ridges on the frontal area. Rounded glabella with subspheroidal L4 and well-incised S1 and S2 glabellar furrows. S3 faintly impressed and oriented inward and slightly forward from axial furrow. Palpebral lobe narrow, ridge-like, located opposite L2 and extending from S1 to just in front of S2. Anterior branches of facial sutures converge forward, producing subtriangular anterior cranial margin in anterior view (e.g., Fig. 15.6).

Occurrence.—Morgan Creek Member (figured specimens collected between 5.5 m and 6.7 m below the top), Wilberns Formation, central Texas (see caption for Fig. 15 for detailed locality information).

Description.—*Ptychaspis occulta* n. sp. is sufficiently similar to *P. matuszaki* n. sp. and *P. bullasa* Lochman and Hu, 1959 that comparisons can be presented in lieu of a full description. *Ptychaspis occulta* and *P. matuszaki* are superficially similar yet differ in detail, and although sample sizes are small, there are clear apomorphic character states that separate them. Diagnostic states for *P. occulta* include more robust sculpture than *P. matuszaki* in both the size and packing density of tubercles, as well as the striate ridges on the frontal area (compare Fig. 15 with Fig. 13.1–13.3); note that the ridges are well defined on internal molds of *P. occulta* (Fig. 15.1–15.3) but are barely perceptible on molds of *P. matuszaki*. *Ptychaspis occulta* also lacks a baccula, and the anterior branches of the facial suture are more rapidly convergent so that the frontal area is subtriangular in anterior view (e.g., Fig. 15.6). By contrast, *P. matuszaki* is bacculate (Fig. 13.1), and the reduced divergence of the facial sutures produces a frontal area that is gently rounded and nearly transverse in anterior view (Figs. 13.3, 14.3).

Ptychaspis occulta differs from *P. bullasa* in having larger, more posteriorly positioned palpebral lobes that are centered opposite L2 (e.g., Fig. 15.4, 15.7) rather than opposite S2 (e.g., Figs. 9.2, 9.6, 9.7, 10.1, 10.4, 10.9). In addition, *P. bullasa* has less-convergent anterior branches of the facial sutures, which yield a more rounded anterior cranial margin (Fig. 9.3, 9.5), whereas *P. occulta* is differentiated further by having larger, more closely spaced tubercular sculpture on the glabella and fixigenae and numerous coarse, striate ridges on the frontal area that are also expressed on the internal mold (Fig. 15.1, 15.4, 15.7).

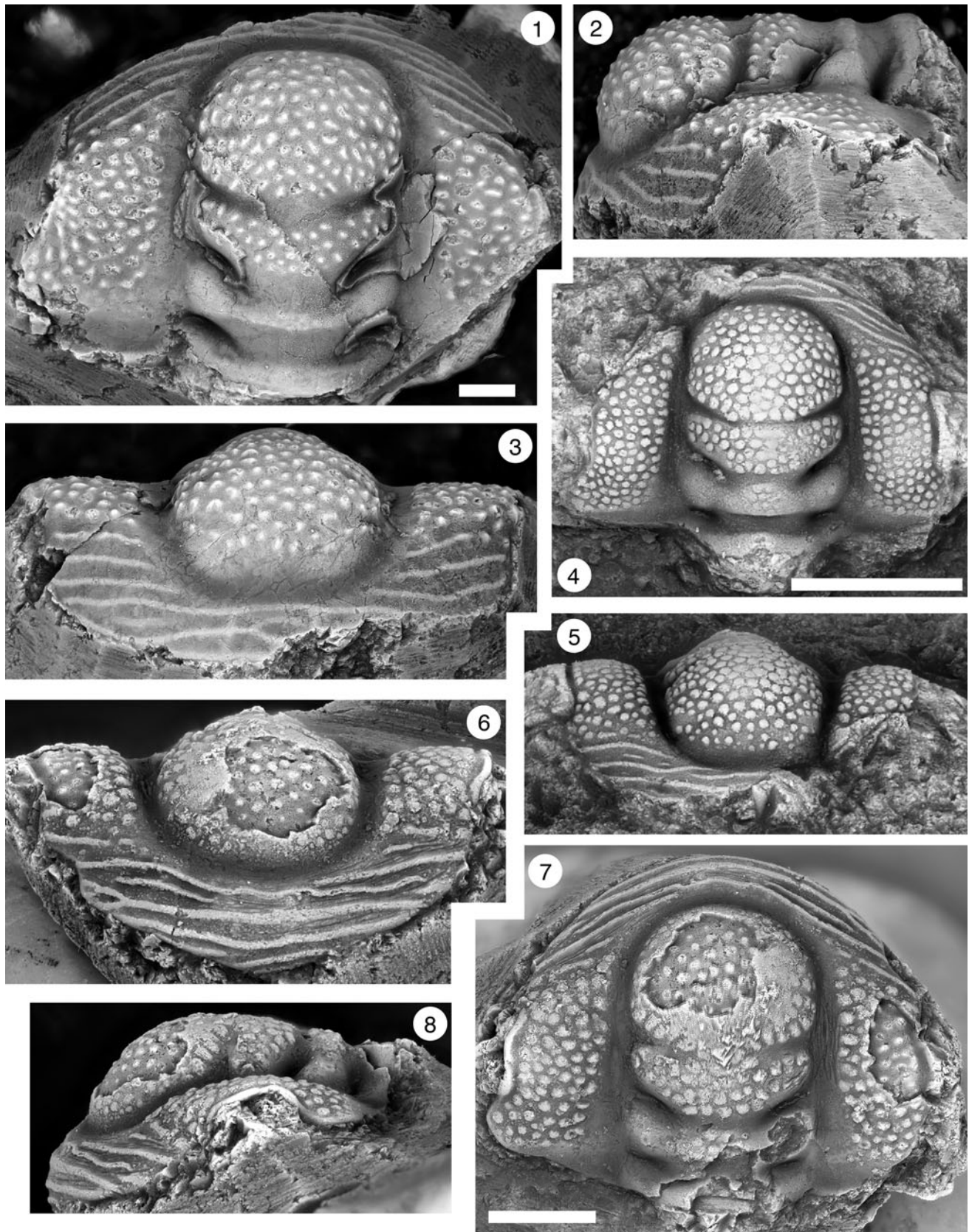


Figure 15. *Prychaspis occulta* n. sp., Morgan Creek Member, Wilberns Formation, central Texas. All are cranidia. (1–3) Paratype USNM 185437, Sudduth section, Burnet County, collection SU 104, about 6.7 m below the top of the Morgan Creek Member (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 17): (1) dorsal view; (2) lateral view; (3) anterior view. (4, 5) Paratype USNM 185470, White Creek section, Blanco County, collection WC 950, about 5.5 m below the top of the Morgan Creek Member (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 14): (4) dorsal view; (5) anterior view. (6–8) Holotype USNM 185472, Little Llano River section, San Saba County, collection LL 725, about 6.4 m below the top of the Morgan Creek Member (illustrated previously by Bell and Ellinwood, 1962, pl. 58, fig. 16): (6) anterior view; (7) dorsal view; (8) lateral view. Scale bars = 2 mm.

Etymology.—From *occulta* (L), “having been hidden,” in reference to the species having gone unrecognized within the literature since 1962.

Remarks.—*Ptychaspis occulta* differs clearly from *P. miniscaensis* (e.g., Bell et al., 1952, pl. 36, fig. 1a, d, e; Westrop, 1986, pl. 8, fig. 15), *Ptychaspis* cf. *P. miniscaensis* (e.g., Westrop, 1986, pl. 7, figs. 1–4), *P. striata* (e.g., Bell et al., 1952, pl. 35, figs. 2b, d, f; Westrop, 1986, pl. 8, figs. 1, 2), and *P. tuberosa* (e.g., Westrop, 1986, pl. 8, fig. 14) in the type of cranidial sculpture. All four of these species lack tubercles; external surfaces and internal molds of *P. striata* and *Ptychaspis* cf. *P. miniscaensis* have coarse, striate ridges over the frontal area, glabella, and fixed cheeks, whereas internal molds of both *P. miniscaensis* and *P. tuberosa* are mostly smooth. In addition, *P. tuberosa* (e.g., Westrop, 1986, pl. 8, fig. 1), *P. striata* (e.g., Bell et al., 1952, pl. 35, figs. 2b, d, f), *P. miniscaensis* (e.g., Bell et al., 1952, fig. 36, fig. 1a), and *Ptychaspis* cf. *P. miniscaensis* (e.g., Westrop, 1986, pl. 7, figs. 1, 4) have smaller, more anteriorly positioned palpebral lobes (centered opposite or just in front of S2 rather than opposite L2) than *P. occulta*. *Ptychaspis granulosa* (e.g., Bell et al., 1952, pl. 35, figs. 1a, e) has a granulose surface but lacks striate ridges, but it has smaller and more anteriorly positioned palpebral lobes (opposite S2) than *P. occulta*.

Ptychaspis sp. 1

Figure 16

Occurrence.—Uppermost Honey Creek and basal Fort Sill formations, section BM, Bally Mountain, Kiowa County, Oklahoma, collections BM 79.4T, BM 80.7, and BM 82.1, *Monocheilus reginae* fauna.

Remarks.—*Ptychaspis* cranidia from section BM are incomplete and cannot be identified to the species level. However, they record what is likely the oldest occurrence of the genus, at the top of the Honey Creek Formation.

Ptychaspis spp.

Figure 17

1970 *Ptychaspis bullasa*; Longacre, p. 44, pl. 2, figs. 4, 5.

Occurrence.—Uppermost Morgan Creek Member (figured specimens collected within a meter of the top), Wilberns Formation, central Texas (see caption for Fig. 17 for detailed locality information).

Remarks.—Longacre (1970) identified two cranidia from the uppermost Morgan Creek Member as *Ptychaspis bullasa*. Not only are they different from the types of *P. bullasa* from Idaho, but they are also clearly distinct from cranidia from lower in the Morgan Creek that we assign to *P. occulta* n. sp. However, the two cranidia differ considerably in size, and contrasts in the anatomy make it difficult to be sure that they record a single species. The smaller of them (Fig. 17.4, 17.5) has large, closely spaced, irregular tubercles confined to the

fixigenae between the posterior border furrow and palpebral ridge. The glabella is smooth, and the long frontal area carries several terrace ridge. The sculpture of small cranidia of *P. bullasa* (Fig. 10.4–10.12) consists of more-numerous, subcircular tubercles that extend over the glabella. Small *P. bullasa* are also characterized by a shorter frontal area and a narrower fixigena that includes a much shorter (tr.) posterolateral projection (e.g., compare Fig. 10.9, 10.10 with Fig. 17.4).

The larger of the cranidia (Fig. 17.1–17.3) has sculpture of rounded tubercles that are more widely spaced than on cranidia of *P. occulta* (Fig. 15) and has fewer terrace ridges on the frontal area. The palpebral lobes are broken off but are almost certainly smaller and more anteriorly positioned than in *P. occulta*, and the portion of the glabella in front of S2 is relatively shorter. Finally, the anterior branches of the facial sutures of this cranidium are not as strongly convergent as in *P. occulta* so that the anterior cranidial margin in anterior view is more transversely oriented. Compared with similarly sized specimens of *P. bullasa* (Figs. 9.1–9.6, 11.1–11.3), tuberculate sculpture extends farther back over the fixigenae, reaching the posterior border furrow, and includes a row of conspicuous tubercles along the posterior border. Further comparisons are hindered by preservation, but palpebral lobes seem to have been in an anterior position, as in *P. bullasa*.

Genus *Wilbernia* Walcott, 1924

Type species.—*Ptychoparia pero* (Walcott, 1890) from the Wilberns Formation of central Texas (by original designation).

Wilbernia cf. *W. diademata* (Hall, 1863)

Figure 18

- cf. 1863 *Conocephalites diadematus* Hall, p. 167, pl. 7, fig. 36, pl. 8, fig. 21 (only).
- cf. 1962 *Wilbernia diademata*; Bell and Ellinwood, p. 365, pl. 34, figs. 9, 10 (synonymy to date).
- cf. 1970 *Wilbernia diademata*; Longacre, p. 32 (synonymy to date).
- cf. 1971 *Wilbernia diademata*; Stitt, p. 33, pl. 3, fig. 2.
- cf. 1986 *Wilbernia diademata*; Westrop, p. 44, pl. 13, figs. 13, 14.

Occurrence.—Honey Creek Formation, section BM, Bally Mountain, Kiowa County, Oklahoma, collection BM 79.4T, *Monocheilus reginae* fauna.

Remarks.—Two nearly complete cranidia possess large palpebral lobes that are equal to about 36% of glabellar length with firmly impressed palpebral furrows. The frontal area consists of a weakly inflated preglabellar field that is slightly shorter than the weakly convex anterior border. They are most like *W. diademata* (Hall, 1863; e.g., Nelson, 1951, pl. 109, figs. 8, 11) but have a shorter border and, consequently, a somewhat shorter frontal area. Cranidia identified as *W. diademata* by Bell and Ellinwood (1962, pl. 54, fig. 9) have shorter palpebral lobes than *Wilbernia* cf. *W. diademata*. Small cranidia attributed to the poorly known *W. halli* Resser, 1937

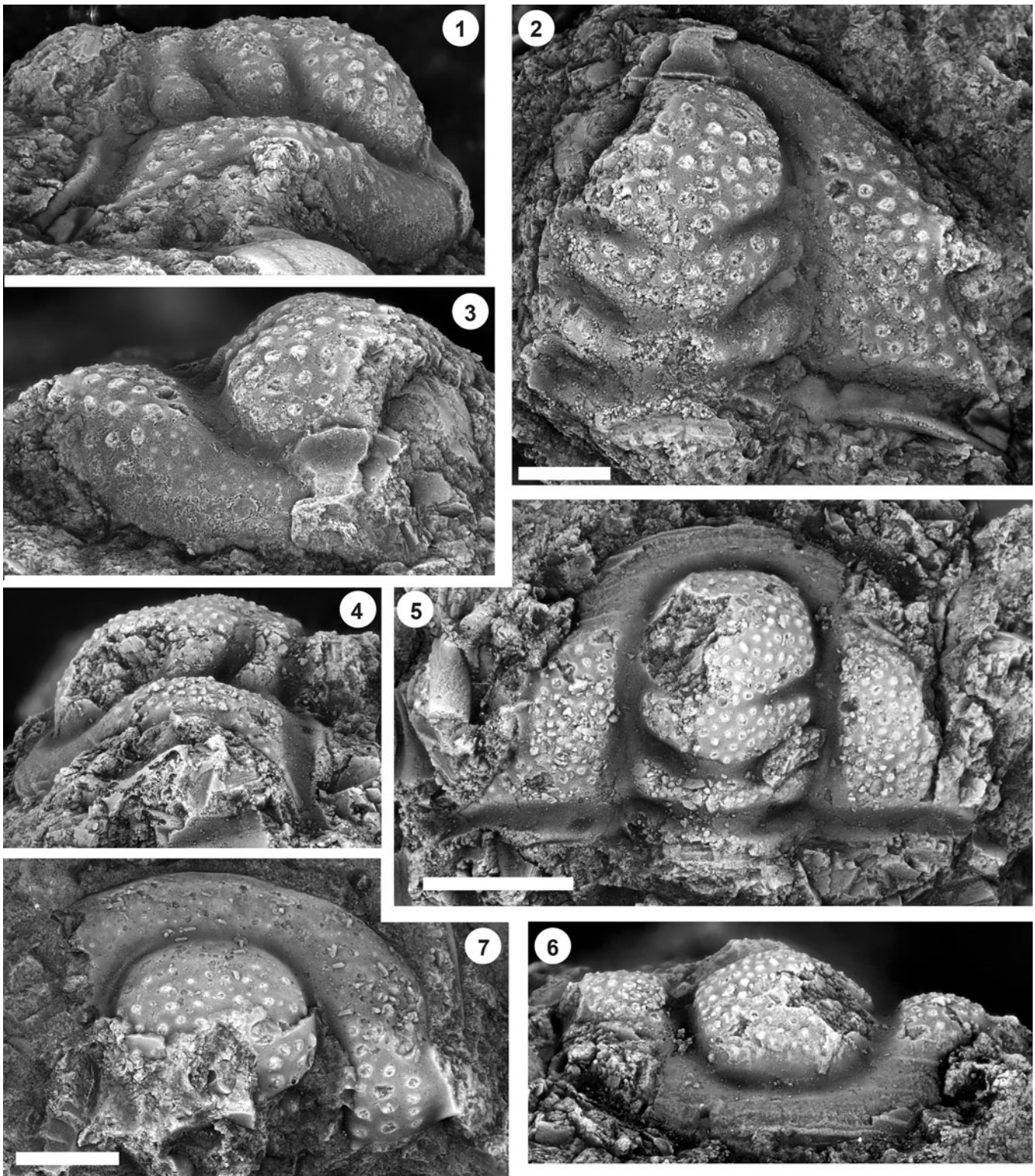


Figure 16. *Ptychaspis* sp. 1, Honey Creek–Fort Sill boundary interval, Bally Mountain section, Kiowa County, Oklahoma. All are crania. (1–3) OU 238381, collection BM 80.7: (1) lateral view; (2) anterior view; (3) dorsal view. (4–6) OU 238171, collection BM 82.1: (4) lateral view; (5) dorsal view; (6) anterior view. (7) OU 238172, dorsal view, collection BM 79.4T. Scale bars = 2 mm.

by both Bell et al. (1952, pl. 32, fig. 5a) and Bell and Ellinwood (1962, fig. 14) approach *Wilbernia* cf. *W. diademata* in frontal area morphology but also have relatively short palpebral lobes. *Wilbernia explanata* (Whitfield, 1880) has a longer frontal

area (Bell et al., 1952, pl. 34, figs. 4b–d; Westrop, 1986, pl. 12, figs. 1, 3), whereas *W. pero* (Walcott, 1890) possesses a preglabellar field that is very short (e.g., Bell and Ellinwood, 1962, pl. 54, fig. 19).

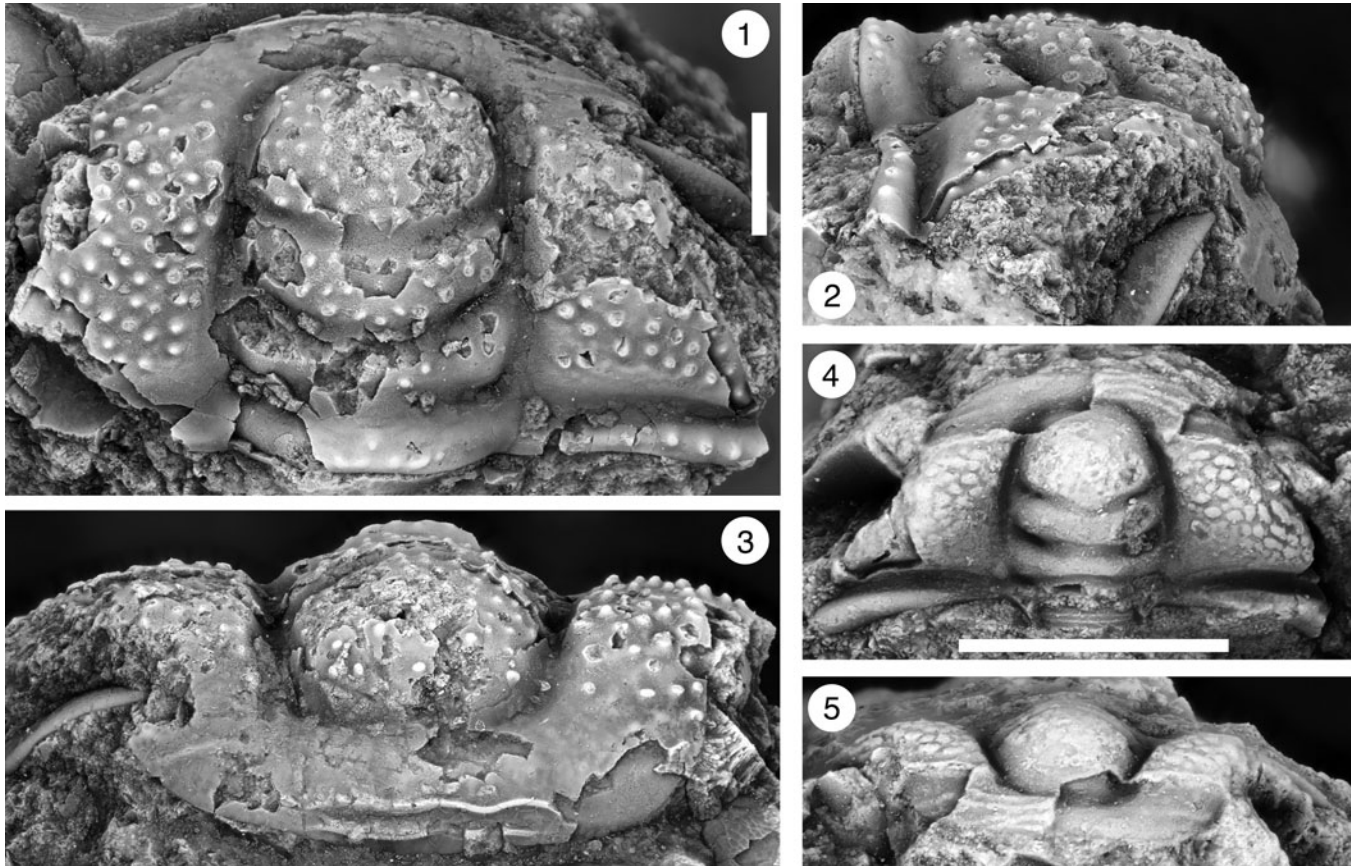


Figure 17. *Ptychaspis* spp., Morgan Creek Member, Wilberns Formation, central Texas. All are cranidia. (1–3) USNM 192202, White Creek section, Blanco County, collection WC 968, at the top of the Morgan Creek Member (illustrated previously by Longacre, 1970, pl. 2, fig. 5): (1) dorsal view; (2) lateral view; (3) anterior view. (4, 5) USNM 192201, Gipson Ranch section, Blanco County collection GR 195, about 0.6 m below the top of the Morgan Creek Member (illustrated previously by Longacre, 1970, pl. 2, fig. 4): (4) dorsal view; (5) anterior view. Scale bars = 2 mm.

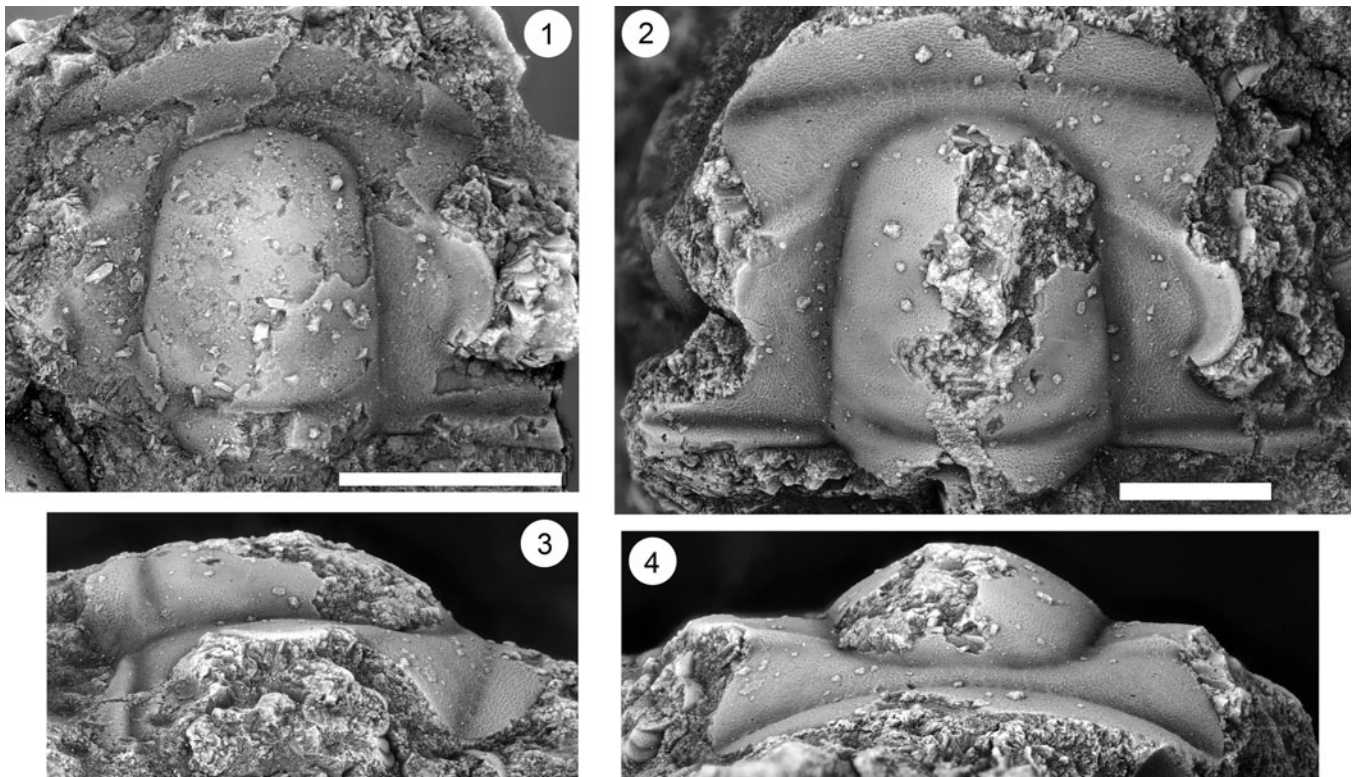


Figure 18. *Wilbernia* cf. *W. diademata* (Hall, 1863) from the Honey Creek Formation, Bally Mountain, Kiowa County. Both cranidia from collection BM 79.4T. (1) OU 238382, dorsal view. (2–4) OU 238170: (2) dorsal view; (3) lateral view; (4) anterior view. Scale bars = 2 mm.

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Declaration of competing interests

The authors declare none.

References

- Adrain, J.M., and Westrop, S.R., 2004, A late Cambrian (Sunwaptan) silicified trilobite fauna from Nevada: *Bulletins of American Paleontology*, v. 365, 56 p.
- Bell, W.C., and Ellinwood, H.L., 1962, Upper Franconian and lower Trempealeuan Cambrian trilobites and brachiopods, Wilberns Formation, Central Texas: *Journal of Paleontology*, v. 36, p. 385–423.
- Bell, W.C., Feniak, O.W., and Kurtz, V.E., 1952, Trilobites of the Franconia Formation, Southeast Minnesota: *Journal of Paleontology*, v. 26, p. 175–198.
- Bucheit, A.K., and Donovan, R.N., 2000, Initiation of a carbonate platform: a comparison between the Lower Jurassic Broadford Limestone, Isle of Skye, Scotland, and the Cambrian Honey Creek Limestone, Slick Hills, Oklahoma: *Oklahoma Geological Survey Circular*, v. 101, p. 57–64.
- Donovan, R.N., 1986, The geology of the Slick Hills, in Donovan, R.N., ed., *The Slick Hills of Southwestern Oklahoma: Fragments of an Aulacogen?*: Oklahoma Geological Survey Guidebook, v. 24, p. 1–12.
- Donovan, R.N., and Bucheit, A.K., 2000, Marine facies and islands in the Reagan Formation (upper Cambrian) in the Slick Hills, southwestern Oklahoma: *Oklahoma Geological Survey Circular*, v. 103, p. 25–37.
- Donovan, R.N., and Ragland, D.A., 1986, Paleozoic stratigraphy of the Slick Hills, southwestern Oklahoma, in Donovan, R.N., ed., *The Slick Hills of Southwestern Oklahoma: Fragments of an Aulacogen?*: Oklahoma Geological Survey Guidebook, v. 24, p. 13–16.
- Donovan, R.N., Ayan, D., and Bucheit, A.K., 2000, Late Cambrian marine-facies transitions: upper member of the Timbered Hills Group, Bally Mountain, Slick Hills, southwestern Oklahoma: *Oklahoma Geological Survey Circular*, v. 103, p. 39–50.
- Frederickson, E.A., 1948, Upper Cambrian trilobites from Oklahoma: *Journal of Paleontology*, v. 22, p. 798–803.
- Frederickson, E.A., 1949, Trilobite fauna of the upper Cambrian Honey Creek Formation: *Journal of Paleontology*, v. 23, p. 341–363.
- Grant, R.E., 1962, Trilobite distribution, upper Franconia Formation (upper Cambrian), southeastern Minnesota: *Journal of Paleontology*, v. 36, p. 965–998.
- Grant, R.E., 1965, Faunas and stratigraphy of the Snowy Range Formation (upper Cambrian) in southwestern Montana and northwestern Wyoming: *Geological Society of America Memoir*, v. 96, 171 p.
- Hall, J., 1863, Preliminary notice of the fauna of the Potsdam Sandstone: 16th Annual Report of the New York State Cabinet of Natural History, p. 119–222.
- Hammer, Ø., Harper, D., and Ryan, P.D., 2001, PAST: paleontological statistics software package for education and data analysis: *Palaeontologia Electronica*, v. 4, no. 1, p. 1–9, http://palaeoelectronica.org/2001_1/past/issue1_01.htm.
- Hu, C., 1971, Ontogeny and sexual dimorphism of lower Paleozoic Trilobita: *Palaeontographica Americana*, v. 44, 155 p.
- Hupé, P., 1953, Contribution à l'étude du Cambrien inférieur et du Précambrien III de l'Anti-Atlas marocain: *Notes et Mémoires de la Service géologique du Maroc*, v. 103, 402 p.
- Lochman, C., and Hu, C.H., 1959, A *Ptychaspis* faunule from the Bear River Range, southeastern Idaho: *Journal of Paleontology*, v. 33, p. 404–427.
- Longacre, S.A., 1970, Trilobites of the upper Cambrian Ptychaspis Biome, Wilberns Formation, central Texas: *Paleontological Society Memoir*, v. 4, 70 p.
- Matuszak, D.R., 1957, *Trilobites from the Fort Sill Formation (upper Cambrian)* [M.S. thesis]: Norman, University of Oklahoma, 55 p.
- Miller, S.A., 1889, North American geology and palaeontology for the use of amateurs, students and scientists: Cincinnati, Western Methodist Book Concern, 718 p.
- Nelson, C.A., 1951, Cambrian trilobites from the St. Croix valley: *Journal of Paleontology*, v. 25, p. 765–784.
- Owen, D.D., 1852, Report of the geological survey of Wisconsin, Iowa and Minnesota: Philadelphia, Lippencott, Grambo and Co., 638 p.
- Raymond, P.E., 1924, New upper Cambrian and Lower Ordovician trilobites from Vermont: *Proceedings of the Boston Society of Natural History*, v. 37, p. 389–465.
- Resser, C.E., 1937, Third contribution to nomenclature of Cambrian trilobites: *Smithsonian Miscellaneous Collections*, v. 95, no. 22, 29 p.
- Resser, C.E., 1942, New upper Cambrian trilobites: *Smithsonian Miscellaneous Collections*, v. 103, 164 p.
- Stitt, J.H., 1971, Late Cambrian and earliest Ordovician trilobites, Timbered Hills and lower Arbuckle Groups, western Arbuckle Mountains, Murray County, Oklahoma: *Oklahoma Geological Survey Bulletin*, v. 110, 83 p.
- Stitt, J.H., 1977, Late Cambrian and earliest Ordovician trilobites, Wichita Mountains Area, Oklahoma: *Oklahoma Geological Survey Bulletin*, v. 124, 79 p.
- Stitt, J.H., and Straatmann, W.M., 1997, Trilobites from the upper part of the Deadwood Formation (upper Franconian and Trempealeuan Stages, upper Cambrian), Black Hills, South Dakota: *Journal of Paleontology*, v. 71, p. 86–102.
- Walcott, C.D., 1890, Description of new forms of upper Cambrian fossils: *Proceedings of the U.S. National Museum*, v. 13, p. 267–279.
- Walcott, C.D., 1916, Cambrian geology and paleontology III no 5. Cambrian trilobites: *Smithsonian Miscellaneous Collections*, v. 64, no. 5) p. 303–426.
- Walcott, C.D., 1924, Cambrian geology and paleontology V., no 2.—Cambrian and lower Ozarkian trilobites: *Smithsonian Miscellaneous Collections*, v. 75, no. 2, p. 1–16.
- Walter, O.T., 1924, Trilobites of Iowa and some related Paleozoic forms: *Iowa Geological Survey Annual Report*, v. 31, p. 169–338.
- Westrop, S.R., 1986, Trilobites of the upper Cambrian Sunwaptan Stage, Southern Canadian Rocky Mountains, Alberta: *Palaeontographica Canadiana*, v. 3, 179 p.
- Westrop, S.R., and Adrain, J.M., 2007, *Bartonaspis* new genus, a trilobite species complex from the base of the upper Cambrian Sunwaptan Stage in North America: *Canadian Journal of Earth Sciences*, v. 44, p. 987–1003.
- Westrop, S.R., and Cuggy, M.B., 1999, Comparative paleoecology of Cambrian trilobite extinctions: *Journal of Paleontology*, v. 73, p. 337–354.
- Westrop, S.R., and Palmer, A.R., 2009, *Wisarcadiaspis*, a replacement name for *Arcadiaspis* Westrop and Palmer, preoccupied: *Journal of Paleontology*, v. 83, p. 316.
- Westrop, S.R., Palmer, A.R., and Runkel, A., 2005, A new Sunwaptan (late Cambrian) trilobite fauna from the upper Mississippi Valley: *Journal of Paleontology*, v. 79, p. 72–88.
- Westrop, S.R., Waskiewicz Poole, R.A., and Adrain, J.M., 2010, Systematics of *Dokimocephalus* and related trilobites from the late Cambrian (Steptoean; Millardian and Furonian Series) of Laurentian North America: *Journal of Systematic Palaeontology*, v. 8, p. 545–606.
- Westrop, S.R., Landing, E., and Dengler, A.A., 2018, Pseudocryptic species of the middle Cambrian trilobite *Eodiscus* Hart, in Walcott, 1884, from Avalonian and Laurentian Newfoundland: *Canadian Journal of Earth Sciences*, v. 55, p. 997–1019.
- Whitfield, R.P., 1878, Preliminary descriptions of new species of fossils from the lower geological formations of Wisconsin: *Annual Report of the Wisconsin Geological Survey for 1878*, p. 50–89.
- Whitfield, R.P., 1880, Descriptions of new species of fossils from the Paleozoic formations of Wisconsin: *Annual report of the Wisconsin Geological Survey for 1879*, p. 44–71.
- Wiley, E.O., 1979, An annotated Linnaean hierarchy, with comments on natural taxa and competing systems: *Systematic Zoology*, v. 28, p. 308–337.
- Winston, D., and Nicholls, H., 1967, Late Cambrian and Early Ordovician faunas from the Wilberns Formation of Central Texas: *Journal of Paleontology*, v. 41, p. 66–96.

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